THE
JOURNAL
OF
RAPTOR RESEARCH

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"To the man who taught me to fly."
M. Herzig, RAMSAR, Mauverney 28, CH-1196 Gland, Switzerland.

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

Frederick N. and Frances Hamerstrom
(Photo by Peter Stettenheim)

PREFACE

This issue of **The Journal of Raptor Research** is in celebration of Frederick and Frances Hamerstrom. By their example and their numerous important contributions they have become an American institution. They have left an impact on the history of American ornithology, on wildlife management, conservation, and on prairie chicken and raptor research, that can never be erased. Why are Fran and Hammi so admired and loved? Because of the example they have set. They never forgot that field research is the naturalist's fountain of knowledge and they never stopped asking searching questions. In contemporary ecology we now probably have far more mathematical models than we have the necessary facts to feed into these models. But the Hamerstroms gathered facts year after year. And they had so much fun doing it that they infected a whole generation of young workers with the same enthusiasm, the same devotion, and the same feeling of doing what makes living worthwhile.

For 59 years Fran and Hammi worked as a team, in the selection of their college courses, in the choice of the research projects, and in the writing up of the results of their work. Between them they authored or co-authored 238

papers and innumerable reviews. After a few years they often could not tell who had written the paper, for one had drafted it and the other one had polished it. Hammi edited all of Fran's ten books and refereed most of the papers sent in by journals in the United States and abroad. Fran handled the papers in German and French and did the more daring aspects of the field work such as the climbing of trees and rocks. Hammi firmly stated, "I prefer to have one foot on the ground." Both of them were particularly proud of a major contribution to science each had made: Hammi developed the scatter-pattern (for managing prairie chickens, a device for preventing fragmentation). Fran discovered that it was not the Northern Harrier (*Circus hudsonius*) who controlled vole abundance but rather that the abundance of the harrier was controlled by the size of the vole population.

Fran and Hammi of course are not merely an American institution. They forged links with ornithologists worldwide. They attended international congresses and made friends everywhere. And let us never forget the selfless dedication with which they, particularly Fran, organized and ran the help for the starving and bombed out European ornithologists after 1945. This quite literally saved lives, because many of them were on the verge of death by starvation. For Fran and Hammi it was simply something "one has to do." They never made any fuss about it, even though they should have received the highest decorations. I am mentioning this aspect of their achievements only to highlight their versatility and their humaneness.

As an old friend and admirer of theirs it gives me the greatest pleasure to write these words of greetings and appreciation. I am delighted that this issue is dedicated in their honor.—**Ernst Mayr, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138.**

FIDELITY TO NESTING TERRITORY AMONG EUROPEAN SPARROWHAWKS IN THREE AREAS

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Abstract.—In three separate study areas, two in south Scotland and one in east-central England, about 70% of European Sparrowhawks (*Accipiter nisus*) trapped in successive years had stayed on the same nesting territory, while the remaining 30% had changed territories between one breeding season and the next. Comparing age-groups, the frequency of territory changes was greatest in 1–2 year birds and became progressively less in 2–3 year and older birds. The figures for the three age-groups were 53%, 29% and 24% in females, and 43%, 36% and 28% in males. Within each age group, birds were more likely to change territory after a nest failure than after a success. A change of territory was usually associated with a change of mate, and followed by an improvement in nest success. The same trends were evident, and the recorded frequencies were remarkably similar, in all three study areas. This was despite the fact that the three areas showed different population trends (one decreasing, another stable and a third increasing), and the most distant areas were separated by more than 350 km.

Fidelidad al territorio de anidar entre gavilanes de la especie *Accipiter nisus,* en tres áreas

Extracto.—En tres áreas de estudio separadas, dos en Escocia y una en la parte central este de Inglaterra, cerca del 70% de gavilanes *Accipiter nisus,* atrapados en años sucesivos, han permanecido en el mismo territorio de anidar; mientras que el 30% restante cambió de territorio entre un ciclo reproductivo y el siguiente. Comparando grupos por edad, la frecuencia en el cambio de territorio fue mayor en aves de 1–2 años, y se hizo progresivamente menor en aves de 2–3 ó más años. Las cifras para los tres grupos por edad fueron 53%, 29%, y 24% en hembras; y 43%, 36%, y 28% en machos. En cada grupo las aves fueron más suceptibles a cambiar de territorio después de un fallido intento de anidar que después de uno con éxito. Un cambio de territorio generalmente estuvo asociado con un cambio de pareja, y estuvo seguido por una mejora en el logro del nido. En las tres áreas de estudio las mismas tendencias fueron evidentes, así también las frecuencias registradas fueron remarcablemente similares. Esto fue así pese al hecho de que las tres áreas mostraron diferentes tendencias de población (una decreciente, otra estable, y la tercera en crecimiento), y las más distantes estaban separadas por más de 350 km.

[Traducción de Eudoxio Paredes-Ruiz]

Like many other birds of prey, European Sparrowhawks (*Accipiter nisus*) often breed in the same restricted localities year after year, creating traditional nesting territories used over long periods (Tinbergen 1946, Newton 1979). Because they feed on a wide range of small birds, sparrowhawks seldom experience marked year-to-year fluctuations in food supply, and in the absence of other major disturbances (see below), their breeding populations tend to remain fairly stable over long periods of years (Newton 1986). In this paper we examine fidelity to territory and mate among sparrowhawks nesting in two areas in south Scotland and in one area in east-central England. Emphasis is placed on the circumstances associated with territory changes and on the consequence of territory changes to both mate fidelity and subsequent nest success. For the two areas in south Scotland the findings largely substantiate those of an earlier analysis of smaller sam-

ples (Newton and Marquiss 1982); for the third area, in east-central England, the findings are presented here for the first time.

In all three areas European Sparrowhawks nested only in woodland, usually building a new nest each year near previous ones. Each year we caught many birds at their nests for banding and identification. We could then check which individuals had remained on the same nesting territories from one year to the next and which had changed territories. Because females were easier to capture than males, we gained much more information for females.

Study Areas

The populations in the three study areas showed different long-term trends. In Annandale, south Scotland (55°15'N 3°5'W), nest numbers in a 700 km² area declined during the 10-yr study from 110 in 1971 to 76 in 1980. This decline was associated with the felling of some well-grown woodland, and the consequent loss of prime nesting

and foraging habitat (Newton and Marquiss 1986). In Eskdale, also in south Scotland (55°16'N 3°25'W), nest numbers in a 200 km² area remained fairly stable, staying within 15% of the mean level of 34 during the 19-yr study (1972–90). This stability in population was associated with relative constancy in habitat. In Rockingham, east-central England (52°30'N 0°30'W), nest numbers in a 220 km² area increased during a 12-yr study from 3 in 1979 to 96 in 1990 (Wyllie and Newton 1991). This increase represented a recovery of the local population following its virtual elimination in the 1960s, probably by organo-chlorine pesticides (Newton and Wyllie 1992). It was not associated with a corresponding change in habitat avail-ability. In all three study areas, nearest-neighbor distances between nesting territories in continuous woodland av-eraged 0.4–0.6 km, but elsewhere were often greater, de-pending largely on the distances between woods.

METHODS

In all three areas all suitable woodland was searched annually for nests, and attempts were made to catch as many breeders as possible. During nest-building, in April and early May, baited cage-traps were placed on the ground near nests, where possible next to regular perches or pluck-ing sites. In this way both sexes could be caught. During incubation in late May and June, females were caught on their nests by use of noose carpets (for this operation, which took about 20 min, the eggs were replaced temporarily by dummy eggs to avoid breakages). As males do not incubate, only females could be caught in this way, but the method was effective only until hatch. In the late nestling and post-fledging stages, in July and early August, further attempts were made to catch breeders using cage-traps. Over the years, most of the females trapped were caught on the nests themselves. We had no evidence that either method of capture affected reproduction, for no differences in mean success were apparent between nests where birds were caught in cage traps, in noose carpets, or not caught at all (Newton 1986).

Sometimes in April we caught more than one male or more than one female near the same nest, making iden-tification of the nest owners uncertain. We therefore stamped an individual number on the flight and tail feath-ers of all birds caught. As sparrowhawks began to molt after egg-laying, their shed feathers were often found near the nest, thus enabling us to check the identity of the incubating female against the one or more females caught earlier at the same site. Most females caught in April, before egg laying, were present on the same territory dur-ing incubation, but some were present on a different (usu-ally neighboring) territory. Moreover, wherever more than one female was caught on the same territory in April, usually no more than one was present during incubation, and often the others were found incubating on other ter-ritories. From more than 2000 nest records, we had only seven instances (0.3%) of two females laying and incu-bating over the same period in the same nest (Newton 1986). The most likely interpretation of these findings is that sparrowhawks are usually monogamous, with one pair per nesting territory, and additional birds caught near nests were neighboring territory owners, non-breeders or other intruders. Because most of the females included in

subsequent analyses were identified at a nest during in-cubation, we could be certain of their eventual affiliation. The same was not true for males, however, whose molted feathers were seldom found. This meant that we could not usually be certain that a male caught near a nest in April did eventually breed there, or when more than one male was caught, which (if any) was the owner.

Because more females than males were captured, fewer data were obtained for males, so records for males from the two Scottish areas were combined. Throughout this paper a nest in which young were raised to fledging is counted as successful, whereas one in which no young were raised is counted as failed, regardless of the stage of failure (in practice most failures occurred at the egg-stage; Newton 1986). In assessing the frequency of territory changes, birds which were forced to move through clear-cutting of their nesting areas were excluded.

RESULTS

Frequency of Territory Changes. The main findings were remarkably similar among areas, even though one was more than 350 km from the other two whose boundaries were only 15 km apart. Among females caught in successive years, 70–75% were on the same territory, while 25–30% had changed ter-ritories between years (Table 1). For females caught at intervals longer than one year, the figures for each area were consistent with an approximate 30% change between years (Table 1).

Dividing females into three age-groups, aged 1, 2 or 3+ yr respectively, revealed a progressive increase in site-fidelity between successive age-groups (Table 2). Overall around 53% of first year females changed territories for the next year, compared with 29% of second year females and 24% of older females. More-over, within each age-group, changes of territory were significantly more frequent after a nest failure than after a success. Again the figures were re-markably similar among areas (Table 2).

The same trends were apparent in males, with (a) about 30% of birds changing territories between years (Table 1), (b) increasing site fidelity with ad-vancing age (43%, 36% and 28% in successive age-groups), and (c) a greater tendency to change ter-ritories after a failure than after a success (Table 2). However, with smaller samples, these trends were seldom significant in particular age-groups or areas. In general, males that changed territories moved over shorter distances than did females (Table 3). Males almost invariably moved to adjacent territories, whereas many females moved to more distant ter-ritories, the record being 28 km from one study area to another. Nonetheless, the majority of moves by both sexes were less than 5 km.

Table 1. Frequency of territory changes (%) among sparrowhawks identified in more than one year. S = stayed on same territory, D = moved to different territory.

| | Birds Retrapped After Minimal Intervals[a] | | | | | | | |
| | One Year | | Two Years | | Three Years | | Four Years | |
	S	D	S	D	S	D	S	D
Females								
Annandale	131 (70)	56 (30)	16	20	4	4	0	2
Eskdale	109 (75)	37 (25)	9	6	1	3	0	1
Rockingham	152 (70)	65 (30)	8	27	2	10	0	3
Males								
Annandale	22 (71)	9 (29)	5	2	2	0	0	1
Eskdale	4 (57)	3 (43)	0	1	1	0	0	0
Rockingham	43 (70)	18 (30)	4	10	2	4	0	3

[a] Different categories are mutually exclusive; percentages are included only for the largest samples of birds caught at one-year intervals

Consequences of Territory Changes. To determine the extent to which change of territory was associated with change of mate, analysis was necessarily restricted to those individuals whose mates were identified in successive years. In all three areas all four possible behavioral patterns were recorded, namely a bird was found in the second year (a) on the same territory with the same mate, (b) on the same territory with a different mate, (c) on a different territory with the same mate, or (d) on a different territory with a different mate. In some instances where a bird had a different mate, the original mate was known to be alive and breeding elsewhere, in other such instances the original mate was known to be dead, but most were of unknown status.

Pooling the overall data for both sexes, some 61% of birds that stayed on the same territory had retained the same mate, whereas only 28% of birds which changed territories retained the same mate (Table 4). All moves in which the pair stayed together were to an adjacent territory. It seems, therefore, that retention of the same territory was more often associated with retention of the same mate than was a change of territory.

As changes of territory were more frequent after a nesting failure than after a success, it was of interest to check whether birds bred more successfully after a move. We therefore examined nest-success before and after a move for all birds which changed territories; similar figures for birds which stayed on the same territories acted as the control. In all three areas, birds that stayed on the same territory had

generally higher success than birds that moved, and often bred less successfully in the second year than in the first (significant in three of fifteen area-age combinations in Table 5). In contrast, birds that changed territory generally bred more successfully in the second year than in the first (significant in three of fifteen area-age combinations in Table 5). Again this tendency was apparent in both sexes. It thus seems that one advantage of a change in territory was an improved chance of nest success.

Discussion

The most striking finding was the consistency in behavior of European Sparrowhawks among areas. In all three areas, about the same proportion of individuals changed territories from year to year and similar relationships were apparent between territory fidelity, previous nest success and age. This consistency occurred, even though the three areas showed different population trends, and one area (Rockingham) was more than 350 km south of the others. Unlike some other raptors, such as the Marsh Hawk (*Circus cyaneus*; Hamerstrom 1969, 1986), the European Sparrowhawk is not noted for nomadism, and most of the movements recorded between territories were less than 5 km. In this respect, too, there was no obvious difference among areas. Probably in all areas the distances recorded were biased towards shorter values, because any birds which left the areas would usually not have been detected. However, the distances that most birds moved were small compared to the dimensions of the study areas.

Table 2. Frequency of territory changes by female sparrowhawks, according to area, age and previous nest success. S = stayed on same territory, D = moved to different territory. Data were from successive years only, the same individual may appear in more than one age comparison.

Area	Age-group	After Previous Nest Success		After Previous Nest Failure		Overall		Significance of Variation Between Successful and Failed Birds (P)
		S	D	S	D	S	D	
Females								
Annandale	1–2	6	3	2	10	8	13	0.03[a]
	2–3	17	3	1	3	18	6	0.04[a]
	3+	89	20	16	17	105	37	<0.001
	All birds (%)	112 (81)	26 (19)	19 (39)	30 (61)	131	56	<0.001
Significance of variation between age-groups		0.49		0.13		0.003		
Eskdale	1–2	4	5	1	4	5	9	0.58[a]
	2–3	17	4	3	8	20	12	0.01[a]
	3+	75	8	9	8	84	16	0.001
	All birds (%)	96 (85)	17 (15)	13 (39)	20 (61)	109	37	<0.001
Significance of variation between age-groups		0.001		0.25		<0.001		
Rockingham	1–2	22	10	2	9	24	19	0.01[a]
	2–3	31	5	3	7	34	12	0.001[a]
	3+	81	20	13	14	94	34	0.002
	All birds (%)	134 (79)	35 (21)	18 (38)	30 (62)	152	65	<0.001
Significance of variation between age-groups		0.20		0.19		0.08		
Males								
Annandale and Eskdale	1–2	2	1	1	0	3	1	1.00[a]
	2–3	4	0	0	3	4	7	0.03[a]
	3+	18	5	4	5	22	10	0.10[a]
	All birds (%)	24 (80)	6 (20)	5 (38)	8 (62)	29 (67)	14 (33)	0.01[a]
Significance of variation between age-groups		0.50		0.16		0.79		
Rockingham	1–2	6	3	4	6	10	9	0.37[a]
	2–3	10	0	2	2	12	2	0.07[a]
	3+	17	4	4	3	21	7	0.32[a]
	All birds (%)	33 (83)	7 (17)	10 (48)	11 (52)	43 (70)	18 (30)	0.01
Significance of variation between age-groups		0.16		0.78		0.09		

[a] F-probabilities calculated by Fisher's Exact Test (two-tailed), otherwise chi-square test was used with Yate's correction. Combined probabilities for all areas, calculated according to Sokal and Rohlf (1981:779–782) were as follows: 1) Behavior in relation to age: after previous success, females $\chi^2 = 18.5$, df $= 6$, $P < 0.01$, males $\chi^2 = 5.09$, df $= 4$, $P < 0.3$; after previous failure, females $\chi^2 = 10.17$, df $= 6$, $P < 0.2$, males $\chi^2 = 4.11$, df $= 4$, $P < 0.5$, overall, females $\chi^2 = 30.61$, df $= 6$, $P < 0.001$, males $\chi^2 = 5.22$, df $= 4$, $P < 0.3$. 2) Behavior in relation to previous nest fate: females aged 1–2 years $\chi^2 = 18.57$, df $= 6$, $P < 0.01$, females aged 2–3 years $\chi^2 = 30.75$, df $= 6$, $P < 0.001$, females aged 3+ years $\chi^2 = 40.06$, df $= 6$, $P < 0.001$, all females $\chi^2 = 41.45$, df $= 6$, $P < 0.001$; males aged 1–2 years $\chi^2 = 1.99$, df $= 4$, $P < 0.8$, males aged 2–3 years $\chi^2 = 12.52$, df $= 4$, $P < 0.02$, males aged 3+ years $\chi^2 = 6.98$, df $= 4$, $P < 0.20$, all males $\chi^2 = 19.28$, df $= 4$, $P < 0.001$.

Table 3. Distances moved by birds which changed nesting territories between successive years. The same individuals may appear in more than one comparison.

| | AGES (YEARS) | NUMBER OF MOVES OF THE FOLLOWING DISTANCES (km) | | | | GEOMETRIC MEAN DISTANCE (km) |
		<1.0	1.1–5.0	5.1–10.0	>10.0	
Females						
Annandale	1–2	2	8	2	1	2.5
	2–3	3	1	2	1	1.8
	3+	12	26	1	1	1.5[a]
Eskdale	1–2	1	7	1	0	2.2
	2–3	2	7	3	0	2.1
	3+	3	13	2	0	1.9
Rockingham	1–2	15	3	1	0	0.8
	2–3	3	8	0	1	2.9
	3+	24	7	2	1	1.8
Males						
Annandale and Eskdale	1–2	1	1	0	0	1.0
	2–3	2	2	0	0	1.0
	3+	9	4	0	0	0.7
Rockingham	1–2	3	2	2	1	1.9
	2–3	2	0	0	0	0.6
	3+	5	2	0	0	0.7

[a] Omits one outlier of 28 km.

In changing territories after nest failure, sparrow-hawks may have been responding to failure as such. Alternatively, both the failure and the move may have occurred in response to some third factor, such as an unsatisfactory local food supply. This would fit with an earlier finding that sparrowhawks were more likely to leave territories with a poor history of occupancy and nest success than territories with a good history of occupancy and nest success (Newton and Marquiss 1982, Newton 1988). As radiotracking showed, the better the food supply the more sedentary sparrowhawks became, and the worse

the food supply the more wide-ranging they became (Newton 1986). Radiotracking further showed that, outside the breeding season, the sexes acted largely independently of one another. It was therefore not surprising that, when individuals changed territories, they usually acquired different mates.

One obvious advantage of site-fidelity to the bird is familiarity with the area, which may enhance foraging success, predator avoidance, defense and other behavior which contributes to reproductive performance. Other things being equal, the longer a sparrowhawk has lived in a locality, the more it

Table 4. Fidelity to mate in relation to fidelity to territory. The figures refer to birds whose mates were identified in two successive years, but the same individuals may appear in more than one comparison.

| BEHAVIOR | ANNANDALE | | ESKDALE | | ROCKINGHAM | | OVERALL | |
	FE-MALES	MALES	FE-MALES	MALES	FE-MALES	MALES	FE-MALES	MALES
On same territory with same mate	13	13	2	2	24	24	39	39
On same territory with different mate	9	14	2	3	12	9	23	26
On different territory with same mate	1	1	2	2	4	4	7	7
On different territory with different mate	6	11	0	1	10	8	16	20

Table 5. Relationship between site-fidelity and subsequent nest success, according to age and area.

	ANNANDALE				ESKDALE				ROCKINGHAM			
	SAME TERRITORY		DIFFERENT TERRITORIES		SAME TERRITORY		DIFFERENT TERRITORIES		SAME TERRITORY		DIFFERENT TERRITORIES	
AGE (YEARS)	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed
Females[a]												
1	6	2	3	10	4	1	4	4	22	2	10	9
2	6	2	10	3	4	1	6	2	14	10	14	5
Significance of variation (P)	1.00[b]		0.02[b]		1.00[b]		0.61[b]		0.02		0.31	
2	16	1	3	3	17	2	4	8	31	3	5	7
3	16	1	3	3	17	2	8	4	29	5	8	4
Significance of variation (P)	1.00[b]		1.00[b]		1.00[b]		0.22[b]		0.71		0.41[b]	
≥3	84	18	21	17	73	10	7	9	81	13	20	14
≥4	71	31	20	18	67	16	14	2	70	24	23	11
Significance of variation (P)	0.05		1.00		0.29		0.03		0.07		0.62	
Overall, one year	106	21 (17)	27	30 (53)	94	13 (12)	15	21 (58)	134	18 (12)	35	30 (46)
Overall, next year	93	34 (27)	33	24 (42)	88	19 (18)	28	8 (22)	113	39 (26)	45	20 (31)
Significance of variation (P)	0.07		0.35		0.34		0.004		0.003		0.11	
Males[a]												
Overall, one year	16	4 (20)	5	6 (55)	3	1 (25)	4	2 (33)	33	7 (18)	7	14 (67)
Overall, next year	15	5 (25)	9	2 (18)	2	2 (50)	5	1 (17)	28	12 (30)	10	11 (52)
Significance of variation (P)	1.00[b]		0.18[b]		1.00[b]		1.00[b]		0.19		0.35	

[a] In each age comparison, the same individuals are represented at both ages.
[b] F-probabilities calculated by Fisher's Exact Test (two-tailed), otherwise chi-square test was used with Yate's correction.

has to lose by leaving it, which may be one reason for the declining tendency to change territories with increasing age. In addition, as a bird ages its social status may rise, increasing its ability to hold a high grade territory and reducing its chance of being displaced by another individual.

In an earlier analysis, based on smaller samples, males changed territories less often than females, but not significantly so (Newton and Marquiss 1982). In the present analysis, based on larger samples, no difference was evident. However, the number of apparent territory changes by males may have been exaggerated if some males were caught while hunting near a neighboring nest. As explained earlier, the affiliation of males to particular nests could not be checked as it could for females. Moreover, virtually all the apparent moves recorded for males were to neighboring territories, whereas many females moved over longer distances. At least in this respect, therefore, males showed greater 'site-fidelity' than females. A difference in site fidelity between the sexes has been noted in a wide range of other birds (Greenwood 1980), including other birds of prey (Newton 1979, Village 1990).

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CAUSES AND CONSEQUENCES OF REVERSED SEXUAL SIZE DIMORPHISM IN RAPTORS: THE HEAD START HYPOTHESIS

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ABSTRACT.—Although a number of hypotheses have attempted to explain reversed sexual size dimorphism (RSD) in raptors, none has gained universal acceptance. Indeed, the function of RSD in predatory birds remains an enigma to many biologists. I present data on the behavioral development of recently fledged Northern Harriers (*Circus cyaneus*) that demonstrate that male fledglings develop more rapidly, and that they leave the immediate vicinity of their nests earlier, and with more flight experience, than do their female counterparts. I use these data, together with those from other published sources, to argue that RSD has evolved in raptors to enable the more rapid development of juvenile males.

My argument is based on the following line of reasoning: male raptors typically provide most, if not all of the prey for both their mates and young during much of the breeding season. Because of this, males, more so than females, must be especially proficient hunters if they are to breed successfully. Both sexes are under intense selection pressure to breed as early in life as possible. Males need to develop hunting skills more rapidly than females to do so. Larger size is not as important in male raptors as it is in other birds because the potentially lethal talons of raptors obviate any benefit accruing to small intra-gender differences in mass. If male raptors were larger, or even the same size as females, their more rapid development would place their female siblings at increased risk of siblicide. By being smaller than their sisters, males reduce this risk, thereby increasing their inclusive fitness, while at the same time enhancing their own development. I call this line of reasoning for the evolution of RSD the "Head Start Hypothesis."

Causas y consecuencias del dimorfismo invertido según el sexo en aves rapaces, la "Hipótesis del Pronto Desarollo"

EXTRACTO.—Aunque numerosas hipótesis se han presentado para explicar el dimorfismo invertido según el sexo, en aves raptoras, ninguna ha ganado aceptación universal. La verdad es que la función de este dimorfismo en aves de rapiña permanece enigmática para muchos biólogos. Presento datos sobre el desarrollo de la conducta de crías, recientemente emplumadas, de las rapaces de la especie *Circus cyaneus*. Estos datos demuestran que las crías machos, recién salidas del nido, se desarrollan más rápidamente y dejan la inmediata vecindad del nido más pronto y con más experiencia en el vuelo que sus hermanas. Hago uso de estos datos, junto con otros procedentes de otras fuentes publicadas, para argüir que el dimorfismo invertido se produce en las rapaces para facilitar el rápido desarollo de los machos jóvenes.

Mi argumento se basa en el siguiente razonamiento: las rapaces machos típicamente proveen la mayor parte, si no todo, de las presas tanto para sus parejas como para sus crías durante buen tiempo de la estación reproductora. Debido a esto, los machos, más que las hembras, deben ser especialmente proficientes en la cacería si es que han de procrear exitosamente. Tanto las hembras como los machos están bajo intensa presión de selección para reproducirse tan temprano en sus vidas como sea posible. Los machos necesitan desarrollar pericia en la caza más pronto que las hembras. El tamaño grande no es tan importante en los machos, como lo es en otra clase de aves, por que sus garras potencialmente letales obvian cualquier beneficio que el tamaño pudiera darles. Si las rapaces machos fueran más grandes, o aun del mismo tamaño que las hembras, su más pronto desarollo total pondría a sus hermanas a un mayor riesgo de ser muertas por ellos. Siendo más pequeños que sus hermanas los machos reducen este riesgo, mientras promueven la sobrevivencia de sus parientes, y al mismo tiempo mejoran su propio desarrollo. Llamo a este raciocinio para la evolución del dimorfismo invertido "Hipótesis del Pronto Desarollo."

[Traducción de Eudoxio Paredes-Ruiz]

For every complex problem there is a simple answer, and it is wrong.

—H.L. Mencken

I introduce my contribution to the Hamerstrom Festschrift with an epigram from Mencken for several reasons. First, Frederick Hamerstrom lived by this credo, and attempted to instill it in his intellectual offspring. Second, Mencken's terse remark certainly applies to the question at hand; to wit, why do predatory birds exhibit reversed sexual size dimorphism (RSD)? And third, Dean Amadon (1975) used this quote to introduce his contribution on the subject of RSD in the Journal of Raptor Research almost two decades ago.

Few would argue that in most species of raptors (i.e., Falconiformes and Strigiformes as recognized by traditional avian taxonomists, see A.O.U. 1983 for North American examples), females are larger than males. However, a consensus on the adaptive value of RSD remains elusive. Indeed, the literature on the subject, which dates from the 13th Century (Wood and Fyfe 1943), is crammed with alternative hypotheses that propose to explain RSD. My own reprint collection on the subject numbers in the hundreds, and Walter (1979), Mueller and Meyer (1985), and Mueller (1990) list more than a dozen hypothetical explanations for the phenomenon. In general, all of the extant hypotheses, most of which can be categorized as ecological, physiological, anatomical, or behavioral adaptations (Table 1; cf., Mueller and Meyer 1985, Mueller 1990), refer to selective forces acting on breeding adults. The latter also appears to be true of hypotheses aimed at explaining RSD in several other avian families (cf., Jehl and Murray 1986).

My purpose here is not to review these hypotheses, nor is it to explain why none has managed to gain overwhelming acceptance. Rather, it is to propose that we investigate the possibility that selective forces acting on developing young and nonbreeding subadults, as well as those acting on breeding adults, are responsible for RSD. Specifically, I use my own research on Northern Harriers (*Circus cyaneus*), along with that of other researchers working on other predatory birds to argue (1) that RSD has important consequences for the developmental biology of raptors and (2) that these consequences need to be considered when attempts are made to determine the cause of RSD in predatory birds. Finally, I propose a new working hypothesis for the evolution of RSD, and suggest ways in which it might be tested.

METHODS

During the summers of 1974–79 I studied the behavioral development of recently fledged Northern Harriers on the 40 000-ha Buena Vista Marsh in Portage County, central Wisconsin, the same site used by Fred and Frances Hamerstrom for their long-term studies of harriers and Greater Prairie Chickens (*Tympanuchus cupido*; Hamerstrom 1986, Hamerstrom and Hamerstrom 1973). Portions of the marsh, which are currently managed for prairie chickens, provide prime nesting habitat for harriers (Hamerstrom 1986, Bildstein 1988). Between 1959 and 1983, 9.6 ± 6.3 (mean $\pm$ SD) pairs of harriers nested on the marsh, including 25, 12, and 25 pairs in 1974, 1977, and 1979, respectively (Hamerstrom 1986). I studied the development of at least 14 unmarked fledglings at five nests in 1974, two individually marked fledglings (one male and one female) at a single nest in 1977, and 29 individually marked fledglings (11 males and 16 females) at seven nests in 1979. In 1977 and 1979, prior to fledging, juveniles were sexed and aged (Hamerstrom 1986) and individually marked by bleaching four adjacent primaries or rectrices (Ellis and Ellis 1975). All marked individuals were watched for from 1–12 hr at least every other day from several days before fledging (i.e., the time of their first brief hovering flights over the nest) until they left the nest area and began to hunt on their own several weeks later (Beske 1982). In 1974, unmarked fledglings were watched for from 30 min to 4 hr 1–4 times a week. Observations, which totaled more than 700 hr over the course of the three breeding seasons, were made using 7× binoculars and a 15× telescope at distances of from 100–250 meters. In 1974 I watched fledglings from the back of a pick-up truck parked on the side of the road, and in 1977 and 1979 I watched them from a portable, lightweight, 2.5-m tower (Bildstein 1980) that I moved among the nest sites.

I used Chi-square extended median tests and student's t-tests to examine the extent of gender-related differences in the behavioral development of fledgling harriers (Siegel 1956, Sokal and Rohlf 1969). Because singleton juveniles are known to develop more slowly than harriers with siblings (Scharf and Balfour 1971, see also Nelson 1977 for a similar phenomenon in Peregrine Falcons *Falco peregrinus*), and because all but two of the fledglings I watched had siblings (the exceptions being the singleton female mentioned above, and a male whose sibling disappeared less than 6 d after his fledging), I limited statistical analysis to broods with more than one nestling.

RESULTS

In 1977 and 1979, 64% (7 of 11) of the marked males and 88% (14 of 16) of the marked females survived to fledging. Males with siblings fledged at 29 ± 2.1 d, while females with siblings fledged at 32 ± 3.8 d ($t = 2.33$, $N = 19$, $P < 0.05$). The sole singleton female fledged at 35 d. Males in all-male broods ($N = 4$) fledged 1.8 d earlier than those in mixed-gender broods ($N = 3$), while females in all-female broods ($N = 4$) fledged 1.4 d later than those

Table 1.   Some of the more popular hypotheses for reversed sexual size dimorphism in raptors based on selective forces acting on breeding adults. Readers interested in the full array of possibilities should consult Mueller and Meyer (1985) and Mueller (1990).

Ecological hypotheses

There are many variations, but, in general, these hypotheses suggest that because raptors of different size feed on prey of different size, RSD acts to reduce food competition in breeding pairs (Storer 1966, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981, Temeles 1985, but see Mueller and Meyer 1985).

Physiological and anatomical hypotheses

Large females lay larger (better?) eggs than do small females (Reynolds 1972, Selander 1972, Cade 1982).

Large females better protect developing follicles during hunting than do smaller females (Walter 1979).

Large females are better incubators than are small females (Snyder and Wiley 1976, Cade 1982).

Large females are better able to withstand periods of food shortage during incubation than are small females (Lundberg 1986).

Small males spend less energy providing food for their young than do large males (Balgooyen 1976).

Behavioral hypotheses

Large females are better protectors of their nests than are small females (Storer 1966, Reynolds 1972, Cade 1982).

Small males are better protectors of their nests than are large females (Andersson and Wiklund 1987).

Large females are better preparers of food for their nestlings than are small females (Andersson and Norberg 1981).

Large females prevent small males from eating their own young (Amadon 1959).

Large females are better able to form and maintain pair bonds than are small females (Mueller and Meyer 1985, Mueller 1990).

Table 2.   Flight activities of fledgling Northern Harriers on the Buena Vista Marsh, 1977 and 1979.

| | PERCENT OF TOTAL | |
TYPE OF FLIGHT	FLEDG-LING WITH SIB-LINGS	SINGLE-TONS
Toward adult carrying prey	12	8
Toward sibling carrying prey	2	
To nest for prey	4	2
Toward adult without prey	8	8
Toward sibling without prey	3	2[a]
In tandem with sibling	17	2[a]
Other[b]	54	78
Total number of flights	758	444

[a] With fledgling from another nest.
[b] Mostly wide, circular "exercise" flights.

meet returning parents with food, which was always transferred aerially to the first fledgling that approached. Although many flights were directed at obtaining prey, either from returning parents or from siblings who had already obtained it from their parents, most flights appeared to be exercising events in which the birds flew in wide circles, either in tandem or by themselves, before returning to their initial perch site (Table 2). Fledglings spent little, if any, time hunting, and although several individuals pounced on and played with inanimate objects, I never saw a fledgling capture live prey during this period.

Males progressed more rapidly than females in all measures of behavioral development. Males took more flights per hour, had longer flight times, and spent more time in the air than females (Fig. 1). Males took their first minute-long flight 9 d earlier than did females, and also first perched at least 50 and 400 m from their nest 4–6 d earlier than did their female counterparts (Fig. 2). By the time males were last seen in the vicinity of their nests, usually at between 43 and 47 d of age, they were spending more than 10 min of each hour in the air. Females, on the other hand were averaging less than 2 min of flight per hour at this age (Fig. 1).

Finally, although I was unable to determine with certainty when each bird left the immediate vicinity of its nest and began to feed on its own, none of the six males that I watched were seen in the vicinity of their nests after they had reached 47 d of age. On

in mixed-gender broods ($N = 10$). Sample sizes, however, were too small to permit statistical analyses.

Once they had fledged, both sexes remained in the vicinity of their nests for an additional two to three weeks, during which time they were fed by their parents. Fledglings were almost always seen perched, usually on fence posts in family groups within 50 m of each other. First flights from the nests typically were brief, vertical springs into the air as a parent, usually the female, returned with food. Within several days of such initial flights, fledglings flew to
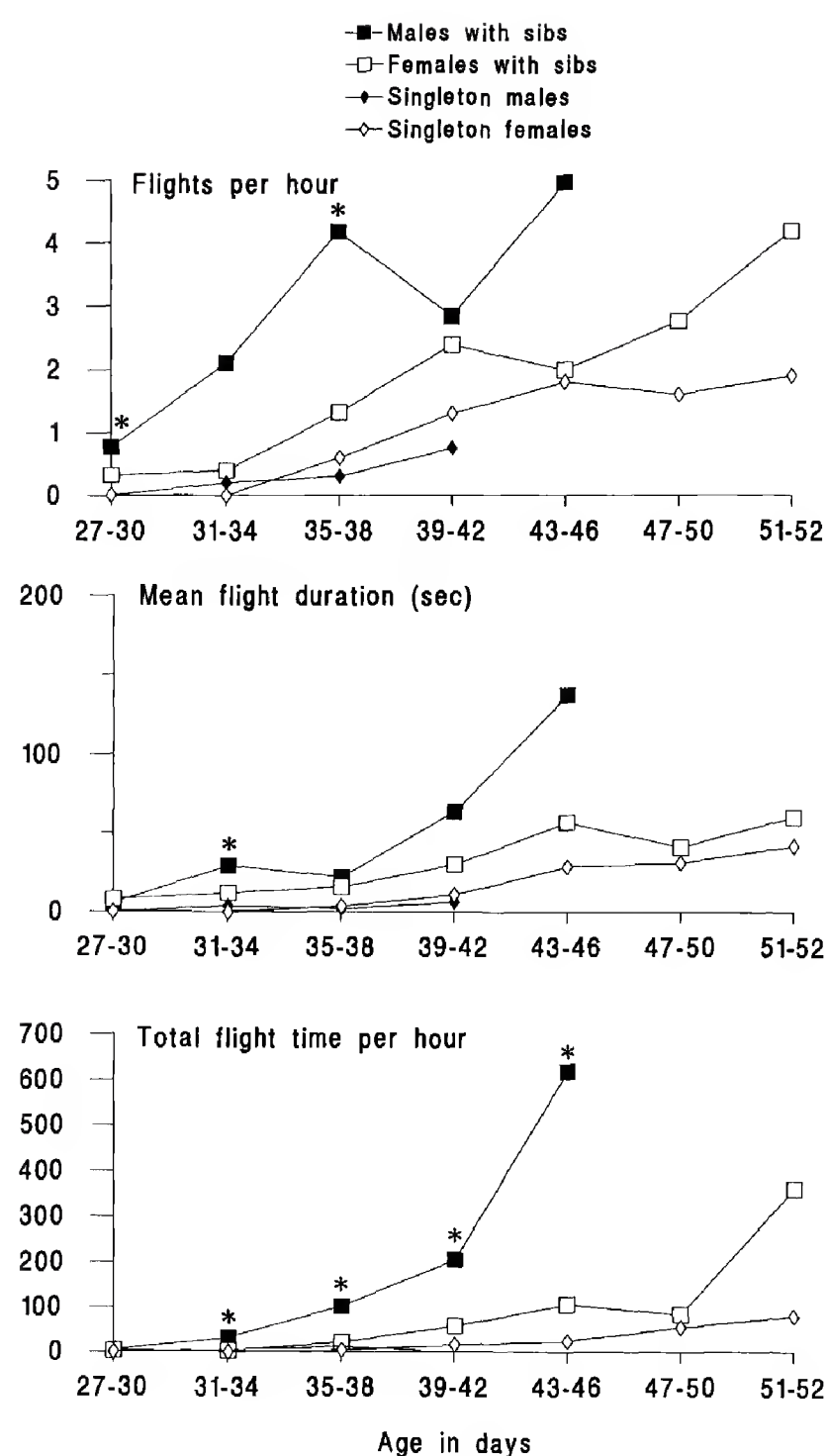
Figure 1. Gender-related differences in the numbers of flights per hour (top), mean flight duration (middle), and total time spent flying per hour (bottom), of fledgling Northern Harriers on the Buena Vista Marsh, central Wisconsin, 1977 and 1979. Significant differences between males and females at multibird nests using Chi-square extended median tests are indicated with asterisks. Data are based on observations of 8 male and 15 female fledglings during a total of 519 hr of observations in 1977 and 1979. Data for males end before those for females because males leave the nest area sooner than females.

the other hand, 9 of 14 females were seen for from 1–6 d beyond this age.

DISCUSSION

My observations clearly illustrate that in Northern Harriers, males develop flight more rapidly, and disperse from their nests earlier and with more flight
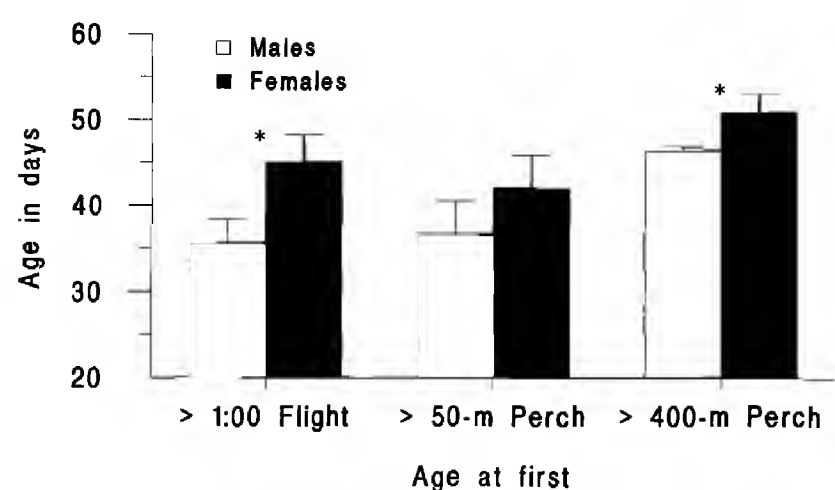

Figure 2. Age in days at which fledgling Northern Harriers first flew for longer than 1 min and perched at least 50 m and 400 m from their nests. Significant differences between males and females at multibird nests using Chi-square extended median tests are indicated with asterisks. Means are indicated by the bars and standard deviations by vertical lines.

experience, than do females. Although post-fledging behavior has been examined in detail in only a few species of raptors, in general, the behavioral patterns I observed in fledgling harriers appear to be similar to those of other species of raptors, including the Osprey (*Pandion haliaetus*; Edwards 1989), Spanish Imperial Eagle (*Aquila heliaca*; Alonso et al. 1987), Eurasian Sparrowhawk (*Accipiter nisus*; Wyllie 1985), Sharp-shinned Hawk (*A. striatus*; Delannoy and Cruz 1988), and Red-tailed Hawk (*Buteo jamaicensis*; Johnson 1986). In general, recently fledged raptors tend to spend most of their time within several hundred meters of the nest waiting for their parents to return with food. Most appear to spend relatively little time hunting on their own during this period, and it is not unusual for a bird to leave the vicinity of the nest and parental care, without having caught a single prey item.

The tendency for males to fledge earlier than their female counterparts appears to be typical of many raptors (Table 3). Similarly, in the two studies that I am aware of that report dispersal times for males and females, male Peregrine Falcons dispersed approximately 4 d earlier than their female siblings (Sherrod 1983); while fledgling male Australasian Harriers (*Circus aeruginosus approximans*) were more "precocious," and left the nest territory about a day earlier than their female counterparts (Baker-Gabb 1978). In captively-reared Eastern Screech-Owls (*Otus asio*), males were more active than young females throughout a 20-week post-fledging period (Ritchison et al. 1992). Overall, then, it appears that my observations of fledgling Northern Harriers in

Table 3. Examples of species for which gender-specific differences in fledging age have been reported.

SPECIES	AGE AT FLEDGING (DAYS)		REFERENCE
	MALES	FEMALES	
Peregrine Falcon	41	44	Sherrod 1983
Sharp-shinned Hawk	24	27	Platt 1976
	28	32	Delannoy and Cruz 1988
Cooper's Hawk (A. cooperii)	30	32–34	Meng 1951
European Sparrowhawk	26	30	Newton 1978
	28	28–30	Wyllie 1985
Hen Harrier	33	38	Balfour 1957
Northern Harrier	29	32	This study
Harris' Hawk (Parabuteo unicinctus)	45	48	Bednarz and Hayden 1991
Bald Eagle (Haliaeetus leucocephalus)	78	82	Bortolotti 1986
Crowned Eagle (Stephanoaetus coronatus)	107	115	Brown 1966

central Wisconsin are similar to those for fledgling raptors elsewhere.

Why do male raptors develop faster than females? I believe that the selective forces acting on males to develop rapidly are greater than those acting on females, and that RSD is the result of this gender-specific difference in selection pressure. Specifically, I argue below that selection favors smaller males because such males develop more rapidly and disperse more quickly, and in better condition, from their nest sites, and that this, in turn, enhances and accelerates their development into breeding adults. I term this explanation for RSD the Head Start Hypothesis.

THE HEAD START HYPOTHESIS AND THE EVOLUTION OF RSD IN RAPTORS

Most raptors hatch their young asynchronously, a phenomenon that has been linked to both sibling competition and brood reduction in a number of species of birds (Lack 1968, but see Magrath 1990 for a thorough review and alternative explanations for hatching asynchrony). And, indeed, both siblicide and brood reduction are common in a number of species of raptorial birds (Newton 1979, Mock 1984). In most instances, smaller siblings, which are dominated by larger sibs, suffer higher mortality as a result of competition for food (cf., Edwards and Collopy 1983). However, in predatory birds, small males reach asymptotic masses and develop flight more rapidly than larger females (Beebe 1960, Moss 1976, Newton 1979, Collopy 1986, Ritchison et al. 1992). In Eurasian Sparrowhawks, for example, sex-specific differences in growth are such that while females outweigh males at fledging, fledgling males

are actually heavier than adult males (i.e., they have already reached asymptotic mass), while fledgling females are considerably lighter than their adult counterparts (Moss 1976). In Golden Eagles (Aquila chrysaetos), nestling males grow and develop at such an enhanced rate that they metabolize as much energy as do their larger female counterparts (Collopy 1986).

The most popular explanation for this phenomenon is that gender-specific growth substantially reduces or nullifies the likelihood of males being outcompeted by their larger female sibs (Newton 1979, Bortolotti 1986, see also Werschkul and Jackson 1979). There are two problems with this initially attractive and seemingly plausible explanation. First, where raptor sibilicide has been examined in detail (cf., Newton 1979), it usually occurs in young nestlings, and almost always within the first half of the nestling period, while male raptors continue to develop behaviorally more rapidly throughout the nestling and fledgling periods, long after this period of vulnerability. Second, and perhaps more importantly, in species of birds where males are larger than females, nestling males almost always require more food than nestling females (e.g., Howe 1977, Cronmiller and Thompson 1981, Linden et al. 1984, Teather 1987, Teather and Weatherhead 1989, see also Slagsvold 1982), at least in part because they, too, typically grow more rapidly than their female counterparts (cf., Linden et al. 1984, Teather 1987). Thus gender-specific differences in adult size alone are not necessarily responsible for gender-specific differences in nestling growth. Nestling males tend to grow and develop faster than nestling females regardless of their relative adult sizes. Viewed in

their entirety, these data suggest that siblicide alone does not explain why small males develop more rapidly than large females.

Why then, do male raptors develop so rapidly? One alternative explanation is that rapid growth and development enables males to breed at an earlier age than they would otherwise be able to do, and that rapid growth and development in females is not equally advantageous.

Most raptors, including Northern Harriers, exhibit delayed maturation, and fail to breed during their second calendar year. Larger species tend to defer breeding longer than do smaller species, and within species (including harriers; Schmutz and Schmutz 1975), males tend to defer longer than do females (Newton 1979). In many non-raptorial birds, delayed maturity has been linked to low reproductive success at earlier ages, in part because of the inferior foraging abilities of younger birds (e.g., Amadon 1964, Lack 1968, Ashmole 1971, Newton 1979, Bildstein 1984). Presumably, hunting skills of younger birds are insufficient to ensure successful breeding, since delayed breeding is more costly to overall fitness than is reduced fecundity (Mac Arthur and Wilson 1967).

Although the development of hunting behavior in recently fledged and prebreeding-age raptors has yet to be studied in detail in most species, evidence suggests that raptors in pre-definitive plumages forage decidedly less efficiently than do adults (Mueller and Berger 1970, Barnard 1979, Bourne 1985, Bildstein 1987). Indeed, Newton (1979) has suggested that "insufficient skill in foraging" may be responsible for the fact that most raptors fail to breed until they are at least 2 yr old.

During both incubation and brooding, male raptors typically provide most, if not all, of the prey for both their mates and developing young (Newton 1979). Females, on the other hand play a major role in providing food for developing young only after brooding has ceased, and females never provide food for both their young and their mates. Thus, becoming a proficient hunter before attempting to breed should be more important for males than for females. Existing data support this notion. In four of the five species in which sexual bimaturism (sensu Wiley 1974) has been reported (Northern Goshawks [Accipiter gentilis], Red-shouldered Hawks [Buteo lineatus], Northern Harriers, and Peregrine Falcons, but not Eurasian Sparrowhawks), males initiate breeding in later years than do females (Newton 1979).

Direct support for the idea that the more rapid development of male raptors enables them to develop hunting skills more rapidly than their female counterparts is scarce. Nevertheless, evidence suggests that birds that fledge and disperse earlier are better prepared for their first winter than are later fledging birds (Hunt and Hunt 1976, Martin 1987, Nilsson and Smith 1988), and that earlier fledging enhances the likelihood of breeding the following spring (Hochachka 1990). Although none of these studies describe the impact of early fledging for males and females separately, all of them support the notion that earlier fledging dates can affect an individual long beyond its survival to independence (cf., Boag and Alway 1980). In addition, several studies suggest that nestling condition is more likely to affect the eventual breeding success of males than of females (Smith et al. 1989, Hochachka and Smith 1991).

I have been able to find only one report in which the impact of fledging date has been examined in detail in predatory birds. However, that investigation also provides evidence in support of the Head Start Hypothesis. In an impressive 7-year study, involving more than 3700 nestling Eurasian Kestrels (Falco tinnunculus), Dijkstra et al. (1990) found that sex ratios (i.e., male : female) declined with hatching date, and, more importantly, that the probability of breeding as a yearling decreased with hatching date for males, but not for females, exactly as suggested by the Head Start Hypothesis.

Any hypothesis that attempts to explain RSD in raptors must also explain why most other species of birds fail to exhibit the same pattern. The Head Start Hypothesis appears to meet this requirement. Nestling raptors are clearly able to kill their siblings, and in a few species do so on a regular basis (Newton 1979). Parental raptors seem indifferent to the siblicidal actions of their offspring (Brown 1971, Steyn 1973). The data presented above demonstrate that male raptors grow and develop more rapidly than their female sibs. If males were also larger, or even if they were the same size as their female counterparts, their presumed more rapid growth and development (see above) would place their female siblings in an especially vulnerable position, not only with regard to siblicide, but also with regard to securing enough prey to fledge successfully. Given these circumstances, reversed size dimorphism enables males to grow and develop more rapidly without unduly threatening their female sibs.

Why, then, don't most other species of birds also exhibit RSD? First, the nestlings of many other species of birds are not normally threatened with

siblicide, nor do they appear to be as prone to starvation as raptors. Furthermore, large adult size in males appears to be more important in other species of birds than it is in raptors (Amadon 1959), possibly because the presence of potentially lethal talons in raptors negates any advantage accruing to a slight difference in mass. (A human example supports the validity of the latter supposition. While prize fighters [i.e., birds without talons] are carefully ranked by weight to equalize the combatants, small soldiers with automatic weapons [i.e., birds with talons] are just as threatening as larger ones.) That several other groups of birds exhibiting RSD (i.e., Sulidae, Stercorariidae) also engage in siblicidal brood reductions (Dorward 1962, Young 1963) lends additional support to the Head Start Hypothesis.

Given the paucity of published information on the behavioral development of fledgling raptors, as well as on the consequences of fledging dates in males and females, this paper, has been quite speculative. Although hypotheses that attempt to explain RSD in raptors are often difficult to test (Andersson and Norberg 1981), the Head Start Hypothesis offers several testable predictions. If the Head Start Hypothesis is true, then: 1) juvenile males should develop hunting skills earlier than their female counterparts. 2) Adult hunting ability should be a more important correlate of initial breeding in males than in females. 3) Early fledging within, as well as across, broods should enhance the probability of early breeding in male, but not female raptors. An experimental test of prediction 3 would be to restrain male fledglings near their nests until after their sisters had fledged, and then compare their flight behavior in subsequent weeks, as well as their breeding success in later years, with those of unconstrained males.

With these predictions in mind, I strongly recommend that additional studies be directed at the least studied portion of raptor life histories: the time between fledging and first breeding. In addition to continuing the long-standing Hamerstrom tradition of focusing one's efforts on pivotal life-history events (see Errington and Hamerstrom 1937), this strategy should foster a better understanding of a phenomenon that has remained unexplained for far too long.

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MOLT OF FLIGHT FEATHERS IN FERRUGINOUS AND SWAINSON'S HAWKS

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ABSTRACT.—Based on 137 breeding Ferruginous and 316 breeding Swainson's hawks, the sequencing and timing of flight feather molt showed great variability. Primary molt preceded secondary and rectrix molt. Different molt centers were discernable among the primaries, in which feather loss proceeded from proximal to distal remiges. Among the secondaries and tertiaries, molt centers were less distinct and direction of feather loss alternated. The hawks differed in the location and number of primary molt centers by species and sex. There was considerable variation both in pattern and timing of molt between wings of the same individuals, between individuals caught in different years, and between parents and offspring. The timing of molt was later in years when reproduction was also later. However, within years the stage of molt was poorly correlated with time of hatch.

Muda de las plumas de vuelo en la raptora de la especie *Buteo regalis* y en la de la especie *Buteo swainsoni*

EXTRACTO.—Basadas en 137 aguilillas de la especie *Buteo regalis* y 316 individuos de *Buteo swainsoni*, ambas especies en su ciclo reproductivo, la secuencia y la época de muda de las plumas de vuelo mostraron gran variabilidad. La muda de plumas primarias precedieron a la de las secundarias y a la de las rectrices. Diferentes centros de muda fueron discernibles dentro de las primarias; en ellos la caída de plumas ocurrió en dirección de adentro hacia afuera del cuerpo. Entre las secundarias y las terciarias los centros de muda fueron menos distinguibles, y la caída de plumas alternó en dirección con respecto al cuerpo. Según la especie y el sexo, estas aves difirieron en cuanto a la ubicación y el número de centros de plumas primarias en muda. Hubo considerable variación tanto en la norma como en la época de muda entre las alas de los mismos individuos; entre individuos cogidos en diferentes años; y entre los padres y sus crías. La época de muda fue retardada en los años en que la reproducción también fue retardada. Sin embargo, dentro de cualquier año, el progreso de la muda de plumas ha sido pobremente correlacionada con la época de empollar.

[Traducción de Eudoxio Paredes-Ruiz]

After fledging from gabboonship (Hamerstrom 1984), my wife Sheila and I attempted to emulate the Hamerstrom approach to field studies of raptors. We equipped ourselves with an 18-column spiral-bound banding book and molt cards (Hamerstrom and Hamerstrom 1971), and began to study competition (Schmutz et al. 1980) and predation (Schmutz et al. 1979) by prairie buteos in Alberta in 1975–77. The Hamerstroms believed in capturing and marking birds (Hamerstrom and Hamerstrom 1973, Hamerstrom 1986) when studying behavior and its interaction with survival and population dynamics. Once a bird was in the hand, it only made sense to them to record as much about it as possible in order to test, in a post hoc *manner, questions posed later. Without being exposed to this philosophy, I probably would not have collected the data described below.*

I compare the molt of flight feathers of Ferruginous (*Buteo regalis*) and Swainson's hawks (*B. swain-*

soni). These two species of hawks may differ in their pattern of molt because they exhibit different migration and breeding schedules (Schmutz et al. 1980). These differences may dictate different rates of overlap in breeding and molt (e.g., Foster 1974) since Swainson's Hawks arrive on their breeding grounds and breed later than Ferruginous Hawks do (Schmutz et al. 1980). Each molt record obtained in this study represented a single point in time. The pattern of molt was deduced from molt records obtained at different times. To my knowledge, molt in Ferruginous Hawks has not been described previously whereas in Swainson's Hawks it has been described only for some captive individuals (Cameron 1913) and for two free-ranging adults (Palmer 1988). Molt data are from breeding adults (≥ 2 years old) and hence the various postulated selective factors important in plumage maturation (e.g., Thompson 1991) probably do not apply here. Since this study represents a comparison of the complex life-history

traits molt and reproduction, where presumed causal links between these traits are evaluated, a number of potential methodological biases discussed by Clutton-Brock and Harvey (1984) are relevant.

STUDY AREA AND METHODS

I recorded the molt of flight feathers (remiges and rectrices) of Ferruginous and Swainson's hawks livetrapped (Hamerstrom 1963) near Hanna, Alberta, between 1975–78 and 1982–91. Primary feathers were numbered 1–10 from the proximal to distal end of the wing, rectrices 1–6 from inner to outer portion of the tail. Secondaries and tertiaries were not differentiated but simply called secondaries from 1–13, distal to proximal. The molt records were taken from Ferruginous Hawks caught during the nestling period of their young between 29 May and 26 July and Swainson's Hawks between 30 June and 25 August. Two Ferruginous and four Swainson's hawks that were caught during laying or incubation were not included in the data sets. Because a large sample of molt records was available for Swainson's Hawks captured in 1983 and thereafter, I used the earlier records only when an individual Swainson's Hawk was captured both before and after 1983. In these analyses, I rejected the null hypothesis when $P < 0.05$.

I analyzed molt of the right wing on a total of 137 Ferruginous and 316 Swainson's hawks. The actual number of molt records used in these analyses varies because in 1984–85 I recorded molt for primaries and rectrices only, and in some cases I could not decide whether a feather was old or new. A feather was recorded: as "old" if it was faded and the edges of the vane worn; as "missing"; as "new" if the distal end of the feather bore a small tip, the edges of the vane were smooth and the rachis contained no blood; as "recent" if the tip of the feather showed only slight fading and wear; or as "growing." For growing feathers, the estimated length was recorded in tenths of the length of adjacent feathers (Hamerstrom et al. 1971). For subsequent analyses the categories new and recent were combined. It is possible that not all feathers were equally readily detected as new. It was difficult to discern replaced from old primaries among the seventh to the tenth because these feathers are most densely pigmented and stiff, the tenth also being shorter. As a consequence, these most distal feathers are less likely to fade or to show wear. However, since missing or growing feathers are identified easily and since their pattern of loss was similar to the pattern of total molt (see Fig. 1 below), this source of error was probably minor.

In addition to presenting data on the molt of individual feathers, I calculated a "molt sum" and recorded "molt centers." Molt sum represents the combined sum of missing feathers (recorded as 0.01), growing feathers (0.1–0.9) and new feathers (1). This sum was calculated for primaries and rectrices separately. Molt centers are groups of missing, growing, new or recent remiges separated by old feathers. The location of a molt center along the wing was identified by the feather with the lowest number. This feather therefore also identifies where molt began within a particular group of molting feathers, since molt in primaries proceeded distally (see below).

The sex of the hawks was determined by body weight. In the case of Ferruginous Hawks, there was no overlap in weight of the sexes. I categorized adults heavier than 1550 g as females (J.K. Schmutz unpubl.). Four Swainson's Hawks fell in the overlap region between 900–950 g and were not categorized to sex. I determined the hatching date of the first nestling by backdating, using a growth curve for primary no. 4 (Schmutz 1977) as the Hamerstroms had done.

RESULTS AND DISCUSSION

One of the functions that a repeated and energetically costly molt may serve is to replace broken feathers that otherwise seriously impede flight (Tucker 1991). Since completed feathers are without a regenerative capacity, a regularly occurring molt seems adaptive. Between 1984–91, 9 (0.5%) of 1952 individual remiges and rectrices on 122 Ferruginous Hawks were broken, 5 of these on the same individual. Seven (0.2%) rectrices and no remiges were broken on 4 of 277 Swainson's Hawks. It is possible that broken feathers are more common than these data suggest, as individuals with broken feathers may be unable either to complete the migration or to join the breeding cohort, and consequently may not appear in the sample analyzed.

Molt Pattern. Both species, but especially Ferruginous Hawks, were molting more of their primaries than either secondaries or rectrices (Fig. 1) at the time of capture. As might be expected, the later nesting and hence later caught Swainson's Hawks were further along in their molt than were Ferruginous Hawks. Apart from a single peak for primary no. 1 (Fig. 1), molt was not simply ascendant or descendant in either of the three groups of flight feathers. Also, the molt pattern is much more complex than data from a few individual Swainson's Hawks (Palmer 1988) imply. Molt often involved more than one molt center and occurred in "waves" termed "serial molt" (e.g., Edelstam 1984) or "Staffelmauser" (Stresemann and Stresemann 1966). Such a wave-like molt was also exhibited by the Common Buzzard (*Buteo buteo*; Bloesch et al. 1977).

Primary no. 1 represented the most important molt center in both species (Table 1). Among some male Ferruginous Hawks, a second molt center was located in the primary 6–8 region (Fig. 1). Among male Swainson's Hawks, two additional molt centers were located in the primary 5–6 and 8–9 regions (Fig. 1). Molt centers were less distinct in the secondaries, but male Swainson's Hawks did show molt centers in the secondary 1, 5 and 11 region, as suggested by Miller (1941).
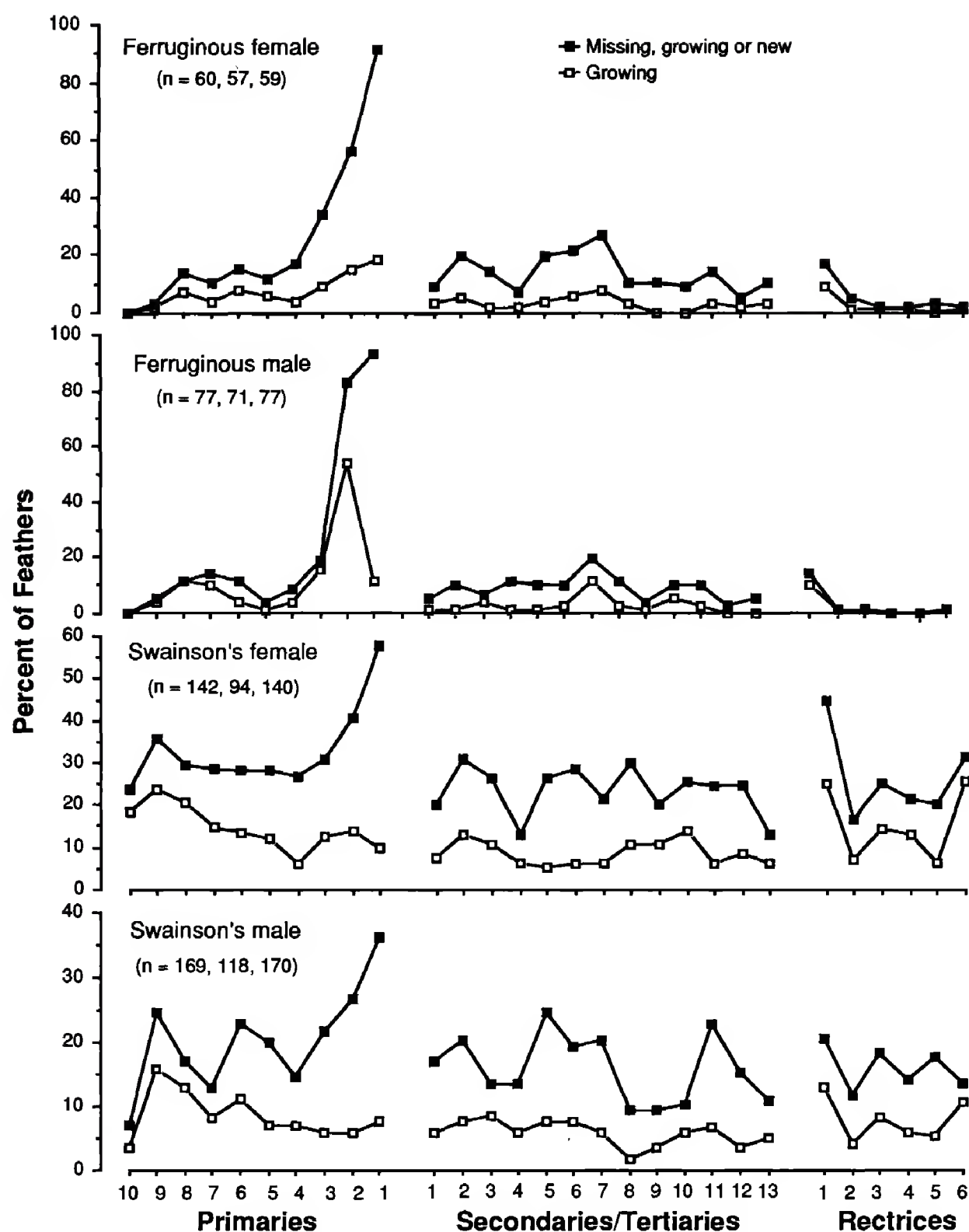
Figure 1.   The percent of feathers of Ferruginous and Swainson's hawks in Alberta in various stages of replacement during the nestling period.

Considering all molt centers, the molt pattern differed between species (G = 18.23, df = 2, P < 0.001). Ferruginous Hawks had always replaced primary no. 1, and on 77% of individuals also feathers in other molt centers, for a maximum of three centers in total. Swainson's Hawks, in contrast, replaced feathers in as many as five molt centers which did not always involve primary no. 1.

Female and male Ferruginous Hawks used the same molt centers, whereas Swainson's Hawks did not. Female and male Ferruginous Hawks showed

molt centers in similar positions (G = 0.57, df = 2, P = 0.753) and of similar number (G = 1.34, df = 2, P = 0.531). More female (74%) than male (34%) Swainson's Hawks involved primary no. 1 (G = 26.06, df = 3, P < 0.001). More female than male Swainson's Hawks also showed more molt centers at the same time (G = 9.11, df = 2, P = 0.018). In another large-bodied bird, the Wandering Albatross (*Diomedea exulans*), breeding females and males also differed in the number of molt centers used, but non-breeders did not differ (Weimerskirch 1991). The

Table 1.   Molt centers in the primary feathers of Ferruginous and Swainson's hawks, arranged first by primary number and then by the number of molt centers. Because the stage of molt could influence the number of molt centers, only those records with a primary molt sum of 2 or higher were included. The resulting average molt sum for Ferruginous Hawks was 2.7 for females, and 2.5 for males, and for Swainson's Hawks 3.2 for females and 2.6 for males.

MOLT CENTER	FERRUGINOUS HAWK		SWAINSON'S HAWK	
	FE-MALE	MALE	FE-MALE	MALE
1	4	12	4	
1, 3	5		1	2
1, 3, 4		1		
1, 3, 5		1		
1, 3, 5, 7, 9				1
1, 3, 5, 8			1	
1, 3, 5, 8, 10			1	
1, 3, 5, 10			1	
1, 3, 6	1			1
1, 3, 6, 8			1	
1, 3, 6, 9			2	
1, 3, 7	1		3	1
1, 3, 7, 10			2	
1, 3, 9			1	1
1, 4	1	2		1
1, 4, 6, 9			1	
1, 4, 7		2	1	
1, 4, 7, 9			1	
1, 4, 8			7	1
1, 4, 9			5	2
1, 4, 10			1	
1, 5	1		2	3
1, 5, 7		1	2	
1, 5, 8	1		2	1
1, 5, 9		1	6	3
1, 6	3	4	7	2
1, 6, 8		2		
1, 6, 9			8	2
1, 6, 10			4	1
1, 7	3	6	5	
1, 7, 9		1	2	2
1, 7, 10			1	
1, 8	5	7	6	2
1, 9	2	3	1	2
1, 10			1	
2	1			
2, 4				1
2, 4, 9			1	
2, 5			1	
2, 5, 7			2	1

Table 1.   Continued.

MOLT CENTER	FERRUGINOUS HAWK		SWAINSON'S HAWK	
	FE-MALE	MALE	FE-MALE	MALE
2, 5, 7, 9			1	
2, 5, 8			1	
2, 5, 9				2
2, 6, 8			1	
2, 6, 9			2	3
2, 6, 10				1
2, 7				1
2, 7, 9			1	
2, 8				2
2, 9				2
3, 5			1	2
3, 5, 10			1	
3, 6, 8				1
3, 6, 9			1	2
3, 6, 10			1	
3, 7			1	
3, 7, 9				1
3, 7, 10			1	2
3, 8			1	3
3, 8, 10			1	1
3, 9			1	
4, 7			1	1
4, 7, 10				1
4, 8				1
4, 8, 10			1	
5, 7, 9				1
5, 8				1
5, 9				1
5, 10			1	
6, 9				3
6, 10				1
8, 10				1
9				1
Total	28	43	102	65

patterns in the hawks studied are consistent with the hypothesis that the later arriving Swainson's Hawks (Schmutz et al. 1980) molt their feathers more rapidly by involving more molt centers than do Ferruginous Hawks. The use of more molt centers may permit a more rapid molt while reducing the size of gaps between feathers.

I deduced the direction of feather loss for each molting group of feathers by recording on which side of a new feather a growing feather was located. For primaries of Ferruginous Hawks, 70 (93%) of 75

growing feathers were on the distal side of a new feather. For Swainson's Hawks the proportion was 69 (92%) of 75. Thus, although not ascendant across all primaries, molt within groups of primaries progressed distally regardless of the location of the molt center. Molting secondaries and tertiaries were more often interspersed with old feathers and hence fewer molting feathers could be found adjacent to new feathers. For both species' secondaries and rectrices combined, 24 (52%) molted inward and 22 outward. This two-directional molt was significantly different from the prevailing outward progression in primaries (G = 41.60, P < 0.001). Secondary and rectrix molt were also not centrifugal as would be indicated by an alternating ascendant and descendant feather loss away from a molt center. Secondary and rectrix molt is perhaps best described as highly variable with molting feathers interspersed with old feathers. Primary molt may be more precisely controlled than either secondary or rectrix molt because the primaries are more important for propulsion (e.g., Welty 1962).

The Timing of Molt. Molt appeared to start during laying or early in incubation. Two Ferruginous Hawks caught during laying or very early in incubation (24–25 April) were replacing primary no. 1 and one was also replacing secondary no. 5. Of three Swainson's Hawks caught 14–24 May, only one was molting, replacing secondary no. 6. A fourth Swainson's Hawk caught during incubation on 17 June, was replacing two primaries, no. 4 and no. 8.

The hawks were highly variable in their progress of primary and rectrix molt as evident from the wide scatter of molt sums during the nestling period (Fig. 2A, 3A). Dolnik and Gavrilov (1980) found that some individual Chaffinches (*Fringilla coelebs*) started their molt up to 4 wk before others. In their study the end of the molt was more synchronous than the beginning, suggesting that molt proceeded at different rates.

To examine whether females and males molted at different rates, I counted the number of data points of male molt sums that were above and below the least-square regression line that best fitted the data points for females. This method is useful because it takes into account the small increase in molt sum over time and because males and females were not always caught on the same dates. Male Ferruginous Hawks had progressed further in their molt, as evident from 46 male sums that were above and 27 below the female's line. This was significantly dif-

ferent from an expected distribution of 50:50 (binomial test, P = 0.012). In contrast, male Swainson's Hawks (16 above and 152 below) molted more slowly than females (P < 0.001), as do harriers (*Circus cyaneus*; Schmutz and Schmutz 1975).

Judging from the slope of the line fitting the molt sum of primaries and rectrices during the nestling period, Ferruginous females and males replaced 0.016 and 0.011 feathers, respectively, in one day. Similarly, Swainson's females and males replaced 0.073 and 0.017, respectively. Extrapolating from these slopes, Ferruginous and Swainson's hawk females and males would require an estimated 1403, 1006, 219 and 941 days, respectively, to replace their primaries and rectrices. Cameron (1913) found that flight feather molt in captive Swainson's Hawks lasted about 6 mo. The unlikely length of time estimated in my study could be explained by 1) a different rate of molt at different times of the year, 2) molt spread over more than 1 yr or 3) a bias in recording new feathers. I was conservative in my judgement of what constituted a new feather. Old feathers often seemed to be of different ages, but it was impossible to distinguish with confidence a feather replaced early in the same or late in the previous year (cf., Edelstam 1984). It is possible that some feathers replaced during incubation faded and wore sufficiently quickly for me to record them as old during the nestling period.

On the study area, Ferruginous Hawks hatched over approximately 2–3 wk and Swainson's Hawks over 4–5 wk (Schmutz et al. 1980). Attempting to explain the great variability in the progress of molt in both species, I plotted molt sum in relation to hatching of the oldest young. This slightly improved the amount of variation explained among female Ferruginous and male Swainson's hawks, but decreased it among male Ferruginous Hawks and female Swainson's Hawks (Fig. 2B, 3B).

Another possible reason for the great spread in molt sums may have been the inclusion of molt data from different years. A comparison of the stage of molt between years is complicated by the different molt sums between the sexes and because the hawks were caught on different dates. To overcome these differences, I expressed the stage of a hawk's molt in terms of deviation, the number of primary and rectrix feather units away from the mean for the particular date (Fig. 2A, 3A). I then compared this deviation between years. The results suggested that, over 4 yr when sample sizes ranged from 17–35,
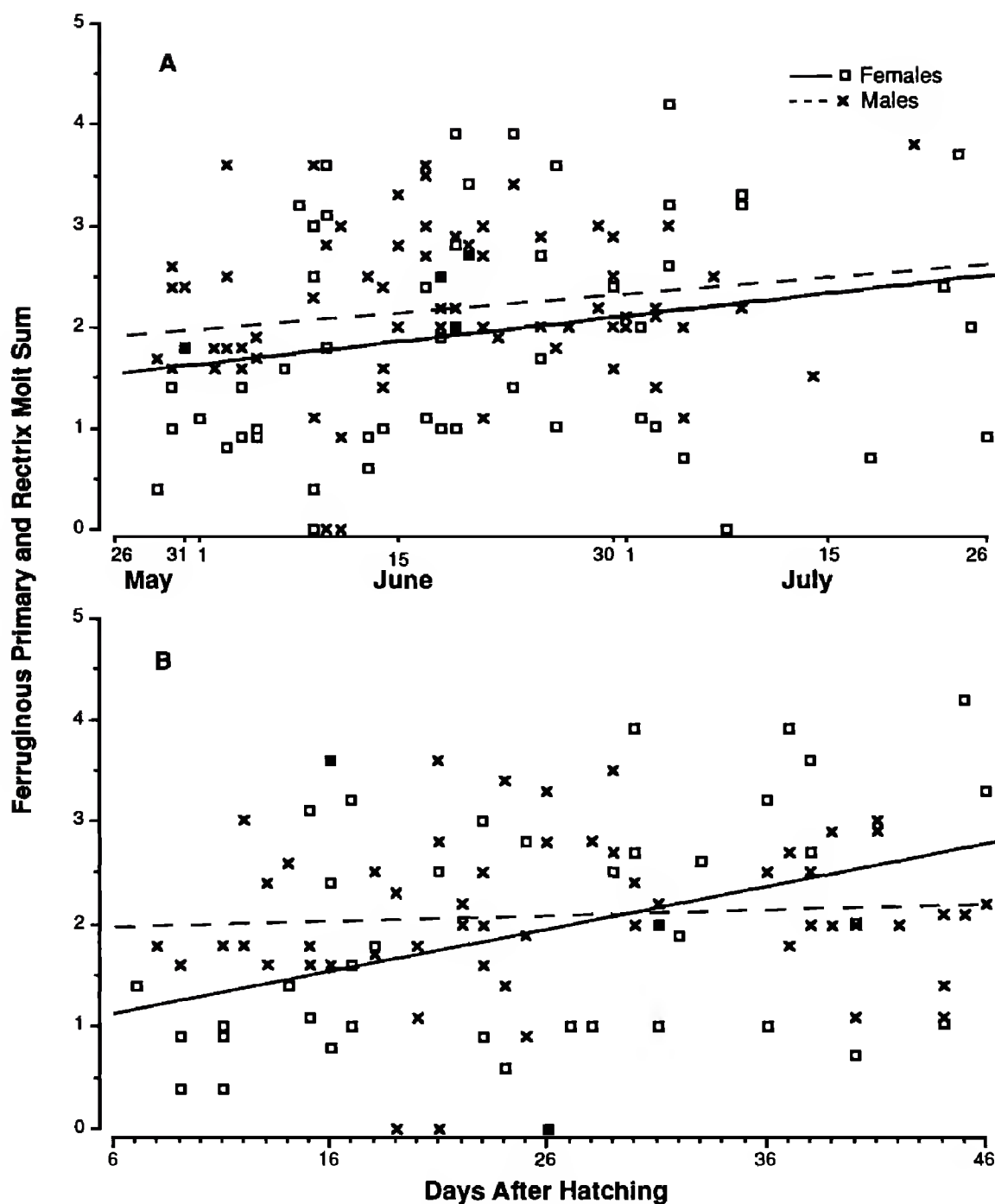
Figure 2.   The sum of primary and rectrix molt of Ferruginous Hawks caught during the nestling period in Alberta, in relation to calender date (A; female r = 0.207, N = 589, P = 0.120 and male r = 0.174, N = 73, P = 0.001) and hatching of the first young (B; female r = 0.400, N = 42, P = 0.008 and male r = 0.073, N = 57, P = 0.590).

Ferruginous Hawks did not differ in their progression of molt (ANOVA F = 1.07, P = 0.365). However, their hatching dates also did not differ (ANOVA F = 1.51, P = 0.217). Swainson's Hawks did differ in their stage of molt (ANOVA F = 4.51, P < 0.001) over 6 yr when sample sizes ranged from 15–94. The Swainson's Hawks' mean hatching dates differed also during those years (ANOVA F = 8.11, P < 0.001). In years when hatching occurred later, molt was delayed (r = 0.828, N = 6, P = 0.042). Thus, while the progress of molt was poorly synchronized with an individual's timing of reproduction within any one year (Fig. 2B, 3B), as a group Swainson's Hawks tended to molt as much as a week later when reproduction was also delayed.

Individual Variability. Although the hawks when considered as a group were highly variable in both the pattern and timing of molt, this could be due to variation between but not necessarily within individuals. I compared differences in molt centers between wings within individuals and between records of the same individual caught in different years. I used only primary molt here since molt in these feathers was most consistent. Intra-individual variation has been considered important by others, and has been used to evaluate heritability of some morphological characters (Falconer 1960). The observation that even within wings of the same hawk there was considerably variability in the sequence in which feathers were lost suggests that feather replacement
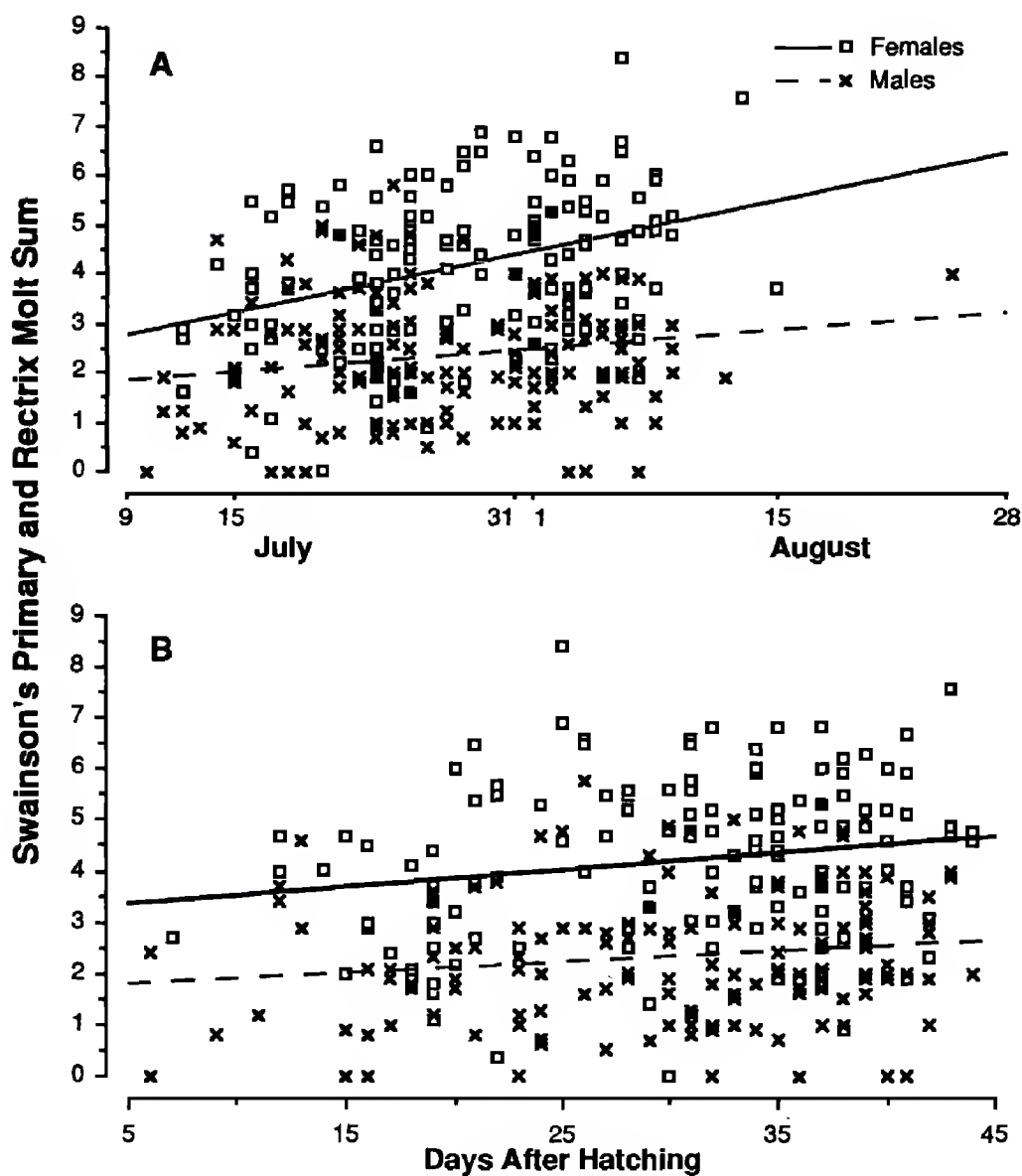
Figure 3.　The sum of primary and rectrix molt of Swainson's Hawks caught during the nestling period in Alberta, in relation to calender date (A; female r = 0.345, N = 141, P < 0.001 and male r = 0.110, N = 164, P = 0.161) and hatching of the first young (B; female r = 0.148, N = 137, P = 0.032 and male r = 0.175, N = 155, P = 0.030).

need not be a precisely regulated biological event. Of 25 individuals of each species selected at random, 11 (44%) Ferruginous (Fig. 4) and 11 (44%) Swainson's hawks (Fig. 5) showed either a different number or location of molt centers between right and left wings.

When comparing molt pattern of the same individual between years, the number of molt centers used could have been confounded by the stage of molt. Since primary no. 1 frequently molted first and other molt centers began later (see Fig. 1), an individual caught early in the season in one year and late in the season in a subsequent year could have shown a different pattern due to differences in time of capture alone. To minimize this potential bias I included molt records of the same individual in successive years only if the molt sum of primaries was within the equivalent of one feather. Using this

restriction, a sample of 9 Ferruginous Hawks and 29 Swainson's Hawks was left for analysis. Both species had either a different number and/or location of molt centers. By scoring the data for both species combined, as having molt pattern the same (molt centers identical in number and position) or different, I found that there was more variation within individuals between years than within individuals between wings (G = 22.49, P < 0.001).

Part of the variation in molt pattern within individuals between years may be due to the hawks completing their molt cycle in a given feather group only in the second year, at which time they may also be initiating a new cycle. Piechocki (1963) found that a 1 yr old, captive Common Buzzard molted primaries 1–8 and retained primaries 9–10. During the following summer, this hawk replaced primaries 1–6 and 9–10, retaining primaries 7–8. In two sub-
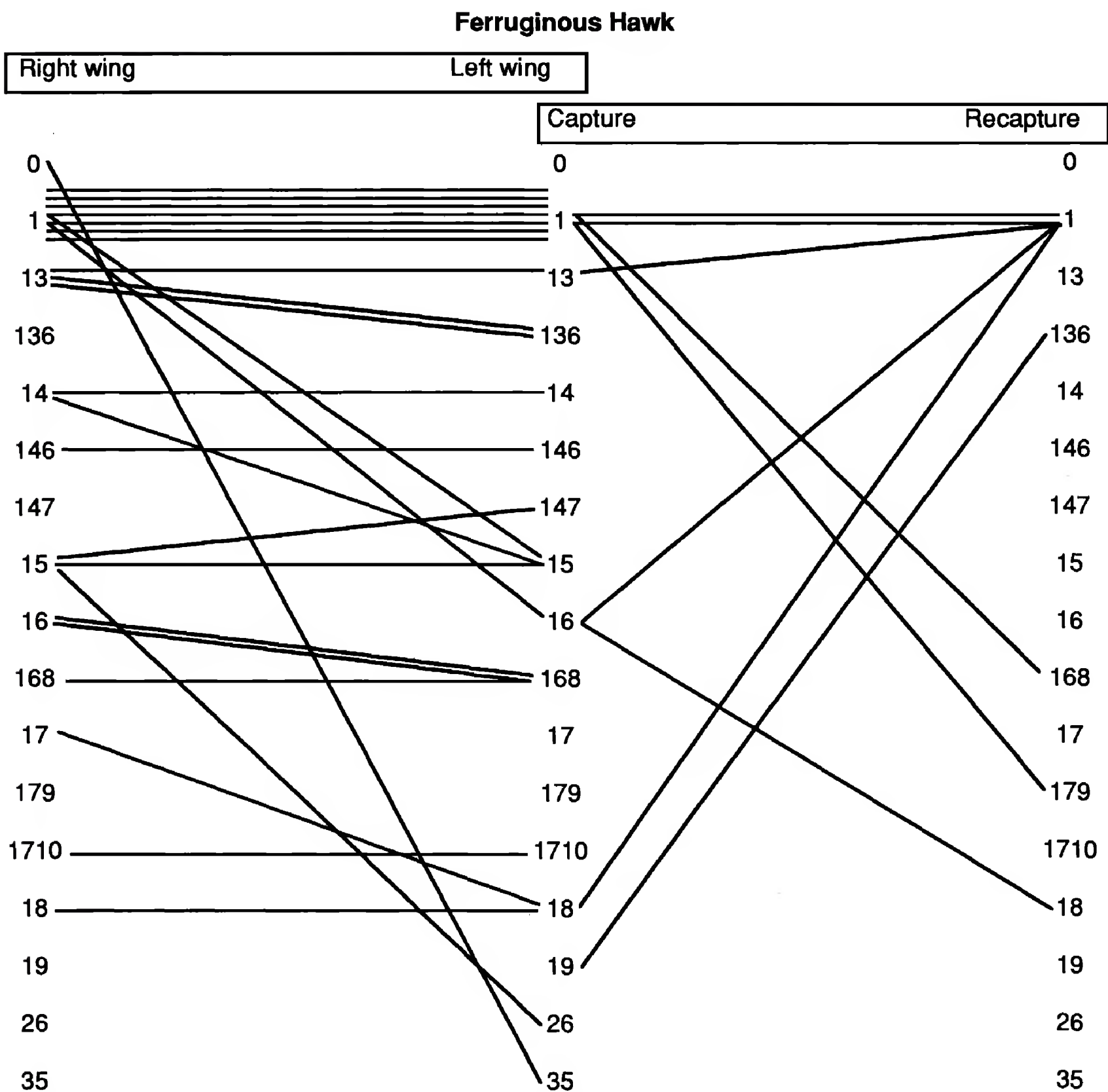
Ferruginous Hawk

Figure 4.   Differences in molt centers (see text) between right and left wings of 25 randomly selected Ferruginous Hawks and between records of 9 breeders caught 1–2 years later.

sequent molt cycles, four and then five different primaries were retained, giving rise to different molt centers and a greater complexity in molt.

Not only did the hawks in this study show different molt centers in different years, but also there was no evidence that timing of their molt was consistent among years. For ten recaptured Ferruginous Hawks, there was no significant correlation between the degree of deviation in molt sums among years ($r = 0.560$, $P = 0.092$). Similarly, the stage of molt measured in molt sum was also not correlated for 52 recaptured Swainson's Hawks among years ($r = 0.010$, $P = 0.943$).

The data presented are based on breeding hawks and hence do not permit a comparison of molt between breeding adults and younger nonbreeders. On
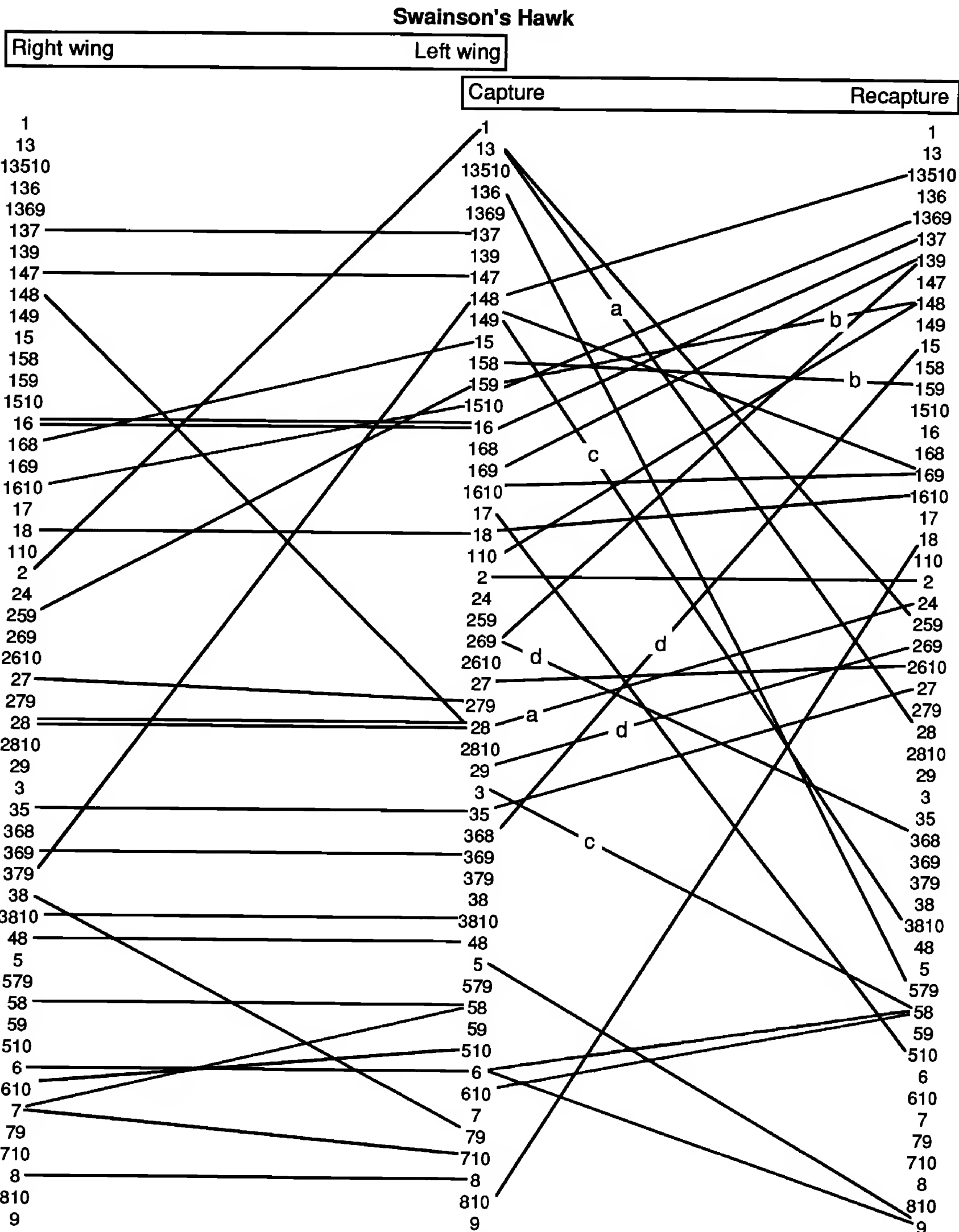
Swainson's Hawk

Figure 5. Differences in molt centers (see text) between right and left wings of 25 randomly selected Swainson's Hawks and between records of 29 breeders caught 1–12 years later. Letters that interrupt lines signify individuals recaptured more than once.

occasion, individual Ferruginous, Swainson's and Red-tailed hawks (*B. jamaicensis*) that frequented the study area showed unusually large gaps in their flight feathers. Such individuals also molted so many body feathers at once that their heads appeared white. I believed that these individuals were young non-breeders, because they did not seem to be associated with a nest and behaved subtly non-territorial and inconspicuous (e.g., Weir and Picozzi 1975). The youngest breeders caught were one male Ferruginous Hawk and one female Swainson's Hawk at the age of 2 yr. The Ferruginous Hawk had a molt sum of 3.2 and a molt center at primary no. 1 and no. 4. The female Swainson's Hawk was perhaps unusual in having only one molt center at primary no. 1 despite a high molt sum of 4.6. Only three other captured females of unknown age had a single molt center at primary no. 1 with a molt sum of 2.0 or higher. It is possible that hawks molting their flight feathers for the first and possibly second time can be distinguished by their molt pattern from older adults, as is the case in the White Stork (*Ciconia ciconia*; Bloesch et al. 1977) and the Barn Owl (*Tyto alba*; P.H. Bloom pers. comm.).

Because each record provided insight into a hawk's molt only at a single point in time, the question of whether these hawks took 2 yr to replace all their flight feathers was not possible to answer unless birds were caught in successive years. Selecting individuals which differed by no more than one feather in their primary molt sum (see above) and were caught in successive years, each of eight Ferruginous Hawks had replaced their primary no. 1 in a successive year. However, none of 11 other molt centers located in more distal positions on the wing in the first year had showed any molt in the second year. Of 42 molt centers in the wings of 17 Swainson's Hawks recaptured 19 times in successive years, 12 (29%) of the molt centers were again molting and 30 were not. These data are sufficient to conclude only that at least some feathers are replaced in successive years. Other feathers not yet replaced at the time of recapture may have been replaced later. Reading (1990) found that a Northern Goshawk (*Accipiter gentilis*) retained one primary for 2 yr in a seven-year study. This hawk retained 45 of 96 secondaries and tertiaries for 2 yr in a six-year period.

Given the degree of variability in the molt of individual hawks between years, it was not surprising to find great variability also between parents and offspring. Among five parents and their four off-spring for each of Ferruginous and Swainson's hawks, there was no indication that similar molt centers were used. Also, parental deviation from the mean molt sum was not correlated with offspring deviation (r = −0.514, N = 10, P = 0.129 for both species combined).

Relationships to Ecological Variables. Pietiäi-nen et al. (1984) found that Ural Owls (*Strix uralensis*) with an above average number of young molted on average fewer feathers at a time. They postulate that the owls balanced energy demands for molting against energy required for reproduction.

There was no evidence of a relationship between molt sum and brood size for Ferruginous or Swainson's hawks. Since brood sizes differed among years (Schmutz and Hungle 1989), I expressed reproductive success in terms of deviation from the yearly mean brood size for the species. I used the number of young raised to near fledging (banding age) making the assumption that this measure reflected the combined territory and individual quality. The correlation between deviation in molt sum and deviation in brood size was r = 0.010 (N = 41, P = 0.950) for Ferruginous Hawk females, r = 0.173 (N = 58, P = 0.194) for Ferruginous Hawk males, r = 0.059 (N = 137, P = 0.492) for Swainson's Hawk females and r = 0.150 (N = 155, P = 0.062) for Swainson's Hawk males. For all but Swainson's Hawk females the sign of the correlation was positive not negative as might be expected. These results are inconsistent with an explanation involving a balancing of energy. Molt sum in harriers was also not correlated with number of young (Schmutz and Schmutz 1975). Morton and Morton (1990) concluded that the control of postnuptial molt in a passerine was independent of reproduction.

The search for a simple negative relationship between molting intensity and reproductive success clearly ignores many subtle constraints that affect energy assimilation and its subsequent expenditure (e.g., Morton and Morton 1990). Even if such a relationship did exist, one could probably construct several plausible scenarios to explain this relationship (cf., Lewontin 1978).

While some molt patterns were apparently repeated with some consistency (e.g., primary molt preceding secondary and rectrix molt, the prevailing use of some molt centers over others, and differences between species and the sexes), the overwhelming conclusion that arises from this study is one of considerable variability in the molt of flight feathers.

There is little doubt that a proper set of feathers is important, first for survival and second for successful reproduction. However, apart from a few basic constraints (e.g., staggering growing feathers to maintain flight capabilities, molting when food is abundant) the pattern by which feathers are replaced may matter little. This may be the case, even if the annual replacement of feathers itself is energetically costly (e.g., King and Murphy 1985).
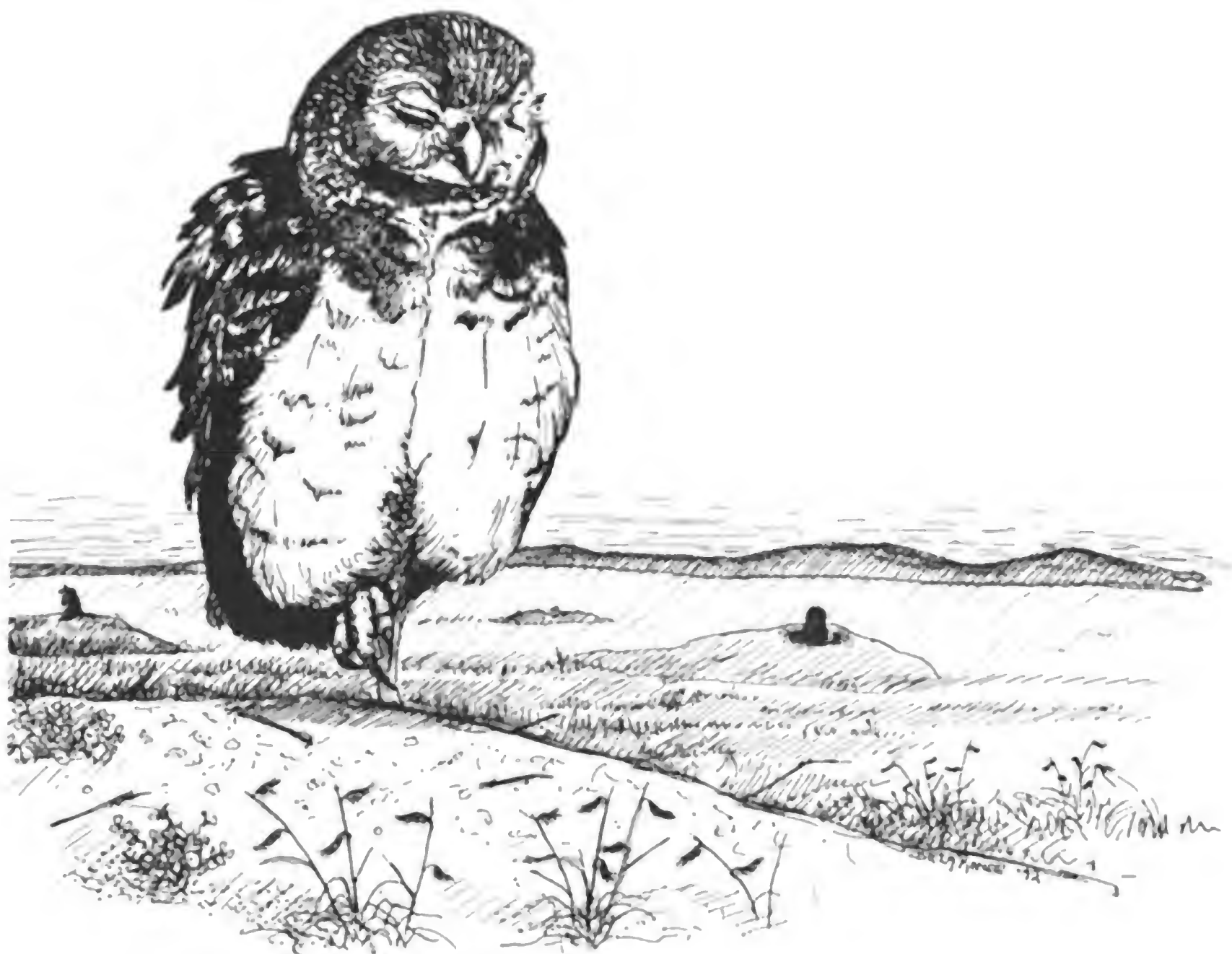
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BEHAVIOR OF MIGRATING RAPTORS: DIFFERENCES BETWEEN SPRING AND FALL

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ABSTRACT.—Forty percent of all raptors observed in spring migration at Cedar Grove, Wisconsin, were southbound (reversed). Northern Harriers (*Circus cyaneus*), Cooper's Hawks (*Accipiter cooperii*), and American Kestrels (*Falco sparverius*) comprised a larger proportion of the migrants in spring than in fall, presumably because they bred at that latitude and many were reorienting and searching for their breeding territories. Raptors migrating in spring attacked birds used as lures in traps more frequently, attacked larger species more frequently and culminated attacks by actually striking the lure more often in spring than in fall. Lure birds which could not flee or become immobile appear as easy prey for raptors. Prey may be scarcer and more experienced in spring than in fall and, thus, easy prey may be more attractive in spring.

Conducta predatoria de aves raptoras migrantes: diferencias entre primavera y otoño

EXTRACTO.—Durante la migración de primavera en Cedar Grove, Wisconsin, 40% de todas las aves rapaces observadas migraron hacia el sur (en sentido contrario). *Circus cyaneus, Accipiter cooperii* y *Falco sparverius* comprendieron la mayor proporción de migrantes durante la primavera comparada con la del otoño, debido a que, presumiblemente, ellos se reproducen en esa latitud y muchos estuvieron reorientándose y buscando sus territorios para su reproducción y cría. En la primavera, las rapaces migratorias atacaron con mayor frecuencia a las aves usadas como señuelo en trampas, ellas atacaron con más frecuencia a las especies más grandes y culminaron sus ataques golpeando efectivamente a los cebos más a menudo en primavera que en otoño. Las aves señuelo, las cuales no pudieron huir ni permanecer inmóbiles, fueron presa fácil para las rapaces. En la primavera, la presa puede ser más escasa y tener más experiencia que en el otoño, resultando por lo tanto que la presa fácil puede ser más atractiva en primavera.

When we first met the Hamerstroms, they were "strictly for the chickens." Dan was an aspiring falconer and Helmut a bird watcher. Hammy helped inspire us to more scientific pursuits and our fascination with raptors led us to start the Cedar Grove Ornithological Station. We spent much time at the Hamerstroms' in the early 1950s and their interests in raptors rekindled as ours developed. Fran and Hammy began visiting Cedar Grove in the mid 1950s and became more and more involved in our activities. Hammy's expertise in carpentry was much appreciated in the building of the station after a fire destroyed the original shanty in 1958. This paper draws upon data that Hammy helped gather, working in a structure he helped design and build.

Most species of raptors are opportunistic and alter their diet as the availability of prey changes. Prey are scarcer, more experienced, and more difficult to obtain in spring than in autumn because there is little or no reproduction in the winter. This paper explores the possibility that the prey preferences of three species of Falconiformes change over the winter and that the probability of attack on three sizes of avian prey might be different in spring migration than in fall migration.

METHODS

Observation and trapping of migrating hawks were conducted in both the springs and autumns of 1953–57 and 1962–65 at the Cedar Grove Ornithological Station in Sheboygan County, Wisconsin. A description of the area can be found in Mueller and Berger (1966), of the trapping methods in Bub (1991), and of the raptor migrations in Mueller and Berger (1961, 1969).

We used domestic pigeons (*Columba livia*, mass 350 g), European Starlings (*Sturnus vulgaris*, mass 80 g) and House Sparrows (*Passer domesticus*, mass 28 g) as lures. Hawks were trapped in bownets if they struck the lure (henceforth, "strikes") or in dho-gazas if they passed over the lure ("passes") or encountered the dho-gaza en route to the lure. In the latter event it is impossible to state whether

or not the raptor might have struck the lure and these hawks were deleted from analyses of strikes and passes. "Attacks" refer to birds that approached our lures closely enough to be captured in bownets or dho-gazas. Some birds approached closely but did not fly into a net or escaped. These events were not recorded consistently, particularly in the 1950s, and are not included in our analyses. Dho-gazas were down more frequently in spring than in fall because of high winds and this might slightly bias the data in favor of fewer passes and more strikes in spring. Pigeons were used as lures on two of our traps. The one used most frequently lacked dho-gazas and could capture birds only in a bownet. There were too few captures in the other trap to permit an analysis of strikes vs. passes and we thus limit these comparisons to attacks on starlings or sparrows.

Seasonal changes in the frequency of attacks on lure birds, in the ratio of attacks on pigeons to attacks on smaller lures and in the ratio of strikes to passes were interpreted as evidence of shifts in prey preference or motivation. We use mass of the captured hawk or falcon as an index of hunger. Birds were weighed in aluminum cylinders to the nearest gram on a triple-beam balance calibrated to 0.1 g.

We selected three species for analysis: Northern Harrier (*Circus cyaneus*), Cooper's Hawk (*Accipiter cooperii*), and American Kestrel (*Falco sparverius*). Together, they account for 50% of raptors observed, and almost 80% of raptors trapped in spring at Cedar Grove. The harrier preys on both birds and small mammals, but it is the latter that predominate when available. The Cooper's Hawk is primarily a specialist on birds, although mammals are also taken. The kestrel feeds on a variety of invertebrates and small vertebrates, but insects, primarily grasshoppers, are the most common prey in late summer and fall, until cold weather forces the birds to shift to a diet consisting of primarily small mammals (see Palmer 1988, or Johnsgard 1990 for a summary of studies of the diet of these species). The dietary habits of the three species leads to the following predictions: kestrels should show the greatest change in prey between fall and spring, harriers less, and there should be little or no change in Cooper's hawks.

Age and sex of the hawks observed but not caught was not consistently determined or recorded. There are possibly age and sex biases in the probability of capture and our data provide little information on the age or sex ratio of migrants. Determining the age of male kestrels is difficult in late fall and almost impossible in spring and we were also inconsistent in our determination of age in the 1950s. The small and possibly biased samples of aged kestrels were not amenable to statistical analysis and we thus divided the sample by sex only.

SYSTAT 5.1 for the MacIntosh (Wilkinson 1989) was used for statistical analysis. Unless otherwise stated, chi-square tests are of 2 × 2 contingency tables with one degree of freedom. Sample sizes differ slightly for the various comparisons because there were occasional omissions and errors in measurement or recording (the latter were deleted) and because some of the original field notes for 1953 have been lost, leaving only a summary of the data.

RESULTS

Five times as many hawks were observed in fall as in spring but only three times as many attacked

lures and were trapped (Table 1). In spring, all three species attacked lures more frequently when southbound than northbound (Fig. 1). Southbound birds in spring attacked lures more frequently than fall migrants (almost all migrants in fall were southbound) but there was no statistically significant difference in the frequency of attacks between fall and northbound spring migrants (Fig. 1). Cooper's hawks and harriers attacked proportionally more pigeons than starlings and sparrows in spring than in fall (Fig. 2). There were no statistically significant differences between spring north- and southbound harriers and Cooper's hawks in the proportions of attacks on the three species of lures. No kestrel attacked a pigeon and too few attacked starlings to permit a statistical comparison with attacks on sparrows. More harriers and kestrels culminated their attacks by actually striking the lure bird in spring than in fall (Fig. 3). Most Cooper's hawks actually struck the lure and too few merely stooped over the lure to permit statistical comparison between seasons.

There was no consistent relationship between mean mass of captured raptors and season. Southbound males in spring were lighter than in fall in all three species but the difference is statistically significant in only two of five comparisons. Northbound males (Fig. 4–6) were lighter than fall migrants in four of five comparisons but none of the differences are statistically significant. In contrast, females were heavier in spring than in fall, both north- and southbound, in kestrels and Cooper's hawks, and significantly so in three of four comparisons in the latter species. However, female harriers conformed to the pattern shown in males and were lighter in spring than in fall in all of four comparisons, and significantly so in two comparisons. Interestingly, southbound raptors of both sexes of all three species were lighter than northbound in all but one of ten comparisons, and the difference is statistically significant in two cases.

Overall, female Cooper's attacked pigeons more frequently than males (Fig. 7), a difference to be expected because of the pronounced sexual dimorphism in size (Fig. 5). But harriers are also very dimorphic (Fig. 4) and there is no difference between the sexes in the frequency of attacks on pigeons (Fig. 7). There were significantly more immatures among southbound harriers than among northbound birds (Fig. 8). Adult harriers attacked pigeons more often than immatures, but there was no age difference in attacks on pigeons in Cooper's hawks (Fig. 7). Note
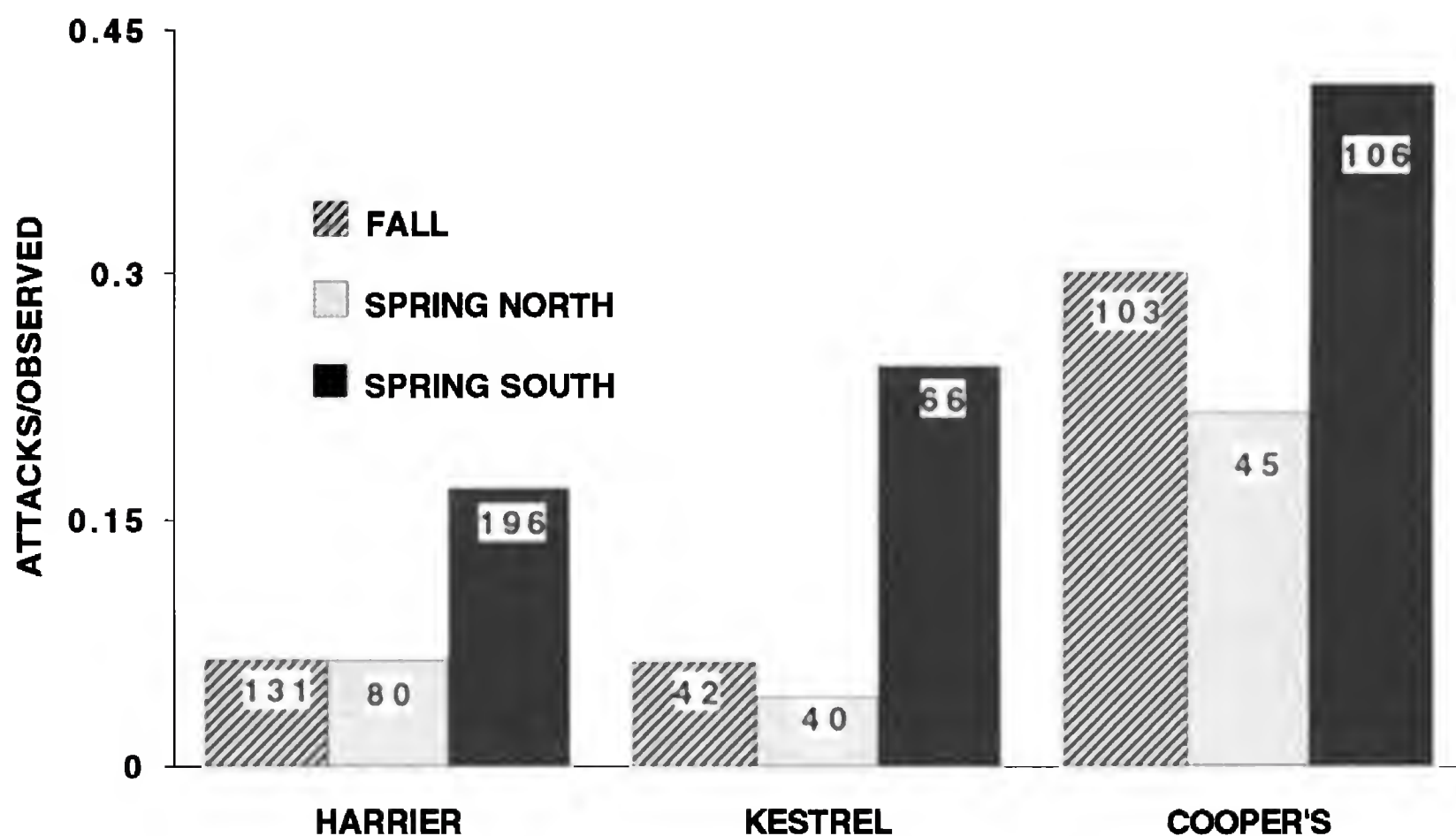
Figure 1.   Proportion of raptors observed that attacked lures. The numbers indicate the number of attacks. Southbound birds in spring attacked more frequently than fall migrants (harrier, $\chi^2 = 71$, $P < 0.0001$; Cooper's, $\chi^2 = 4.11$, $P < 0.05$; kestrel, $\chi^2 = 46$, $P < 0.0001$). Southbound birds attacked more frequently than northbound birds (harrier, $\chi^2 = 53$, $P < 0.0001$; Cooper's, $\chi^2 = 11.1$, $P < 0.0009$; kestrel, $\chi^2 = 84$, $P < 0.0001$). No other differences within species are statistically significant ($P > 0.05$).

that the data in Fig. 7 are for spring only. Both species attack proportionately more pigeons in spring than in fall (Fig. 2) and this analysis had to be restricted to one season. Spring was chosen because too few adult harriers attacked pigeons in fall to permit statistical analysis (1 of 14 adults, 6 of 115 immatures).

DISCUSSION

Five times as many hawks were observed in fall at Cedar Grove as in spring but 40% of the spring migrants were southbound and probably more than a few of these were already counted going north. There are a variety of factors that might explain the differences between spring and fall in the number of migrant raptors observed. The shoreline of Lake Michigan acts as a leading line concentrating water-shy raptors (Mueller and Berger 1967). Locally, the shoreline is oriented NNE-SSW, considerably more effective in concentrating south- than northbound migrants. Lake Michigan is very cold in spring and the air over it is cooled accordingly. A shallow layer of cold, dense air often extends inland, often for

several hundred meters and occasionally for several kilometers, persisting even in the face of a moderately strong westerly wind if the air inland is warm. The warm air slides up and over the cold air, creating a line of updrafts. These updrafts can be utilized by raptors and would concentrate them some distance inland and often beyond the view of our observation blind. On a larger scale, the shoreline of Lake Michigan is much better oriented for concentrating south- than northbound migrants. The average orientation of the shoreline to the outskirts of the Milwaukee metropolitan area, 34 km away, is 15° west of south. A line drawn south of Cedar Grove extends over Lake Michigan for 52 km before making a brief landfall north of Racine, Wisconsin, the next brief landfall is near Zion, Illinois, 118 km south, and continuous passage overland is not attained until the metropolitan Chicago area, 150 km south. The southern end of Lake Michigan is not much farther south. The large cities of Chicago, Milwaukee and the considerable urban development between them further inhibit the concentrating effects of the shoreline on migration (Mueller and Berger 1967). In
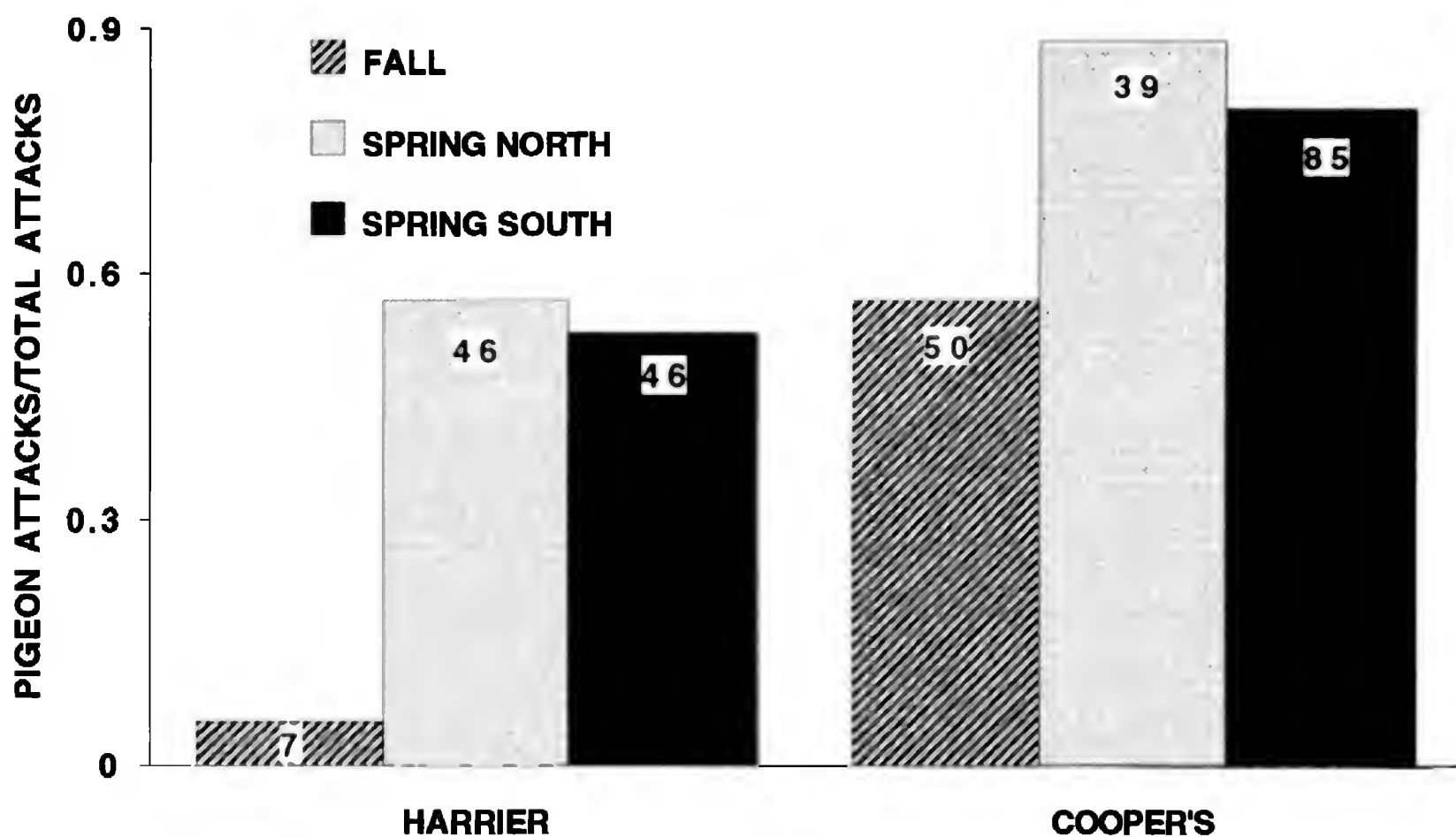
Figure 2.   Attacks on pigeons as a proportion of all attacks on lures. The numbers indicate the number of attacks on pigeons. Raptors attacked pigeons more frequently in spring than in fall (harriers: northbound, $\chi^2 = 78$, $P < 0.0001$; southbound, $\chi^2 = 70$, $P < 0.001$. Coopers': northbound, $\chi^2 = 13.5$, $P < 0.003$; southbound, $\chi^2 = 12.4$, $P < 0.005$). No kestrel attacked a pigeon.

contrast, a line drawn north from Cedar Grove never again strikes the main body of Lake Michigan, and variously effective leading lines of Lake Michigan and Green Bay reach to the upper peninsula of Michigan 240 km to the north.

The number of hawks observed at Cedar Grove is only an index of the number of migrants passing through the region. The weather, particularly wind direction, strongly influences the concentration of migrants along the lakeshore (Mueller and Berger 1961). Hawks southbound in spring have previously migrated north that season and may have been counted at Cedar Grove as northbound migrants. Indeed, it is possible that some migrants were counted several times in one season but this is unlikely to occur often because conditions suitable for bringing migrants over the station occur only sporadically. Southbound birds are considerably more likely to occur at Cedar Grove than northbound birds because of the greater effectiveness of leading lines to the north. It is thus difficult to compare the numbers of hawks seen in fall and spring. The best comparison is obviously between northbound spring birds and (southbound) fall birds but the former is obviously an underesti-

mate, or the latter an overestimate, of the number of hawks passing through the region because of the differences in the leading lines in the two directions.

In absolute numbers, more harriers and Cooper's hawks were seen in fall than were seen northbound in spring, but almost half again as many kestrels were seen northbound in spring as southbound in fall. A migratory direction west of south in fall and east of north in the spring would result in more kestrels being concentrated on the western shore of Lake Michigan in spring than in fall. If this is true, we might expect that band recoveries of kestrels to the south of Cedar Grove should be concentrated to the west. A cursory examination fails to reveal an obvious pattern but final judgment awaits a detailed examination. Although the numbers of harriers and Cooper's hawks observed northbound at Cedar Grove in spring do not exceed the numbers seen in fall, it is probable that they also are present along the lakeshore in spring in excessive numbers and require an explanation similar to what we have tentatively proposed for kestrels.

Broad-winged Hawks (*Buteo platypterus*) and Sharp-shinned Hawks (*A. striatus*) are the most com-
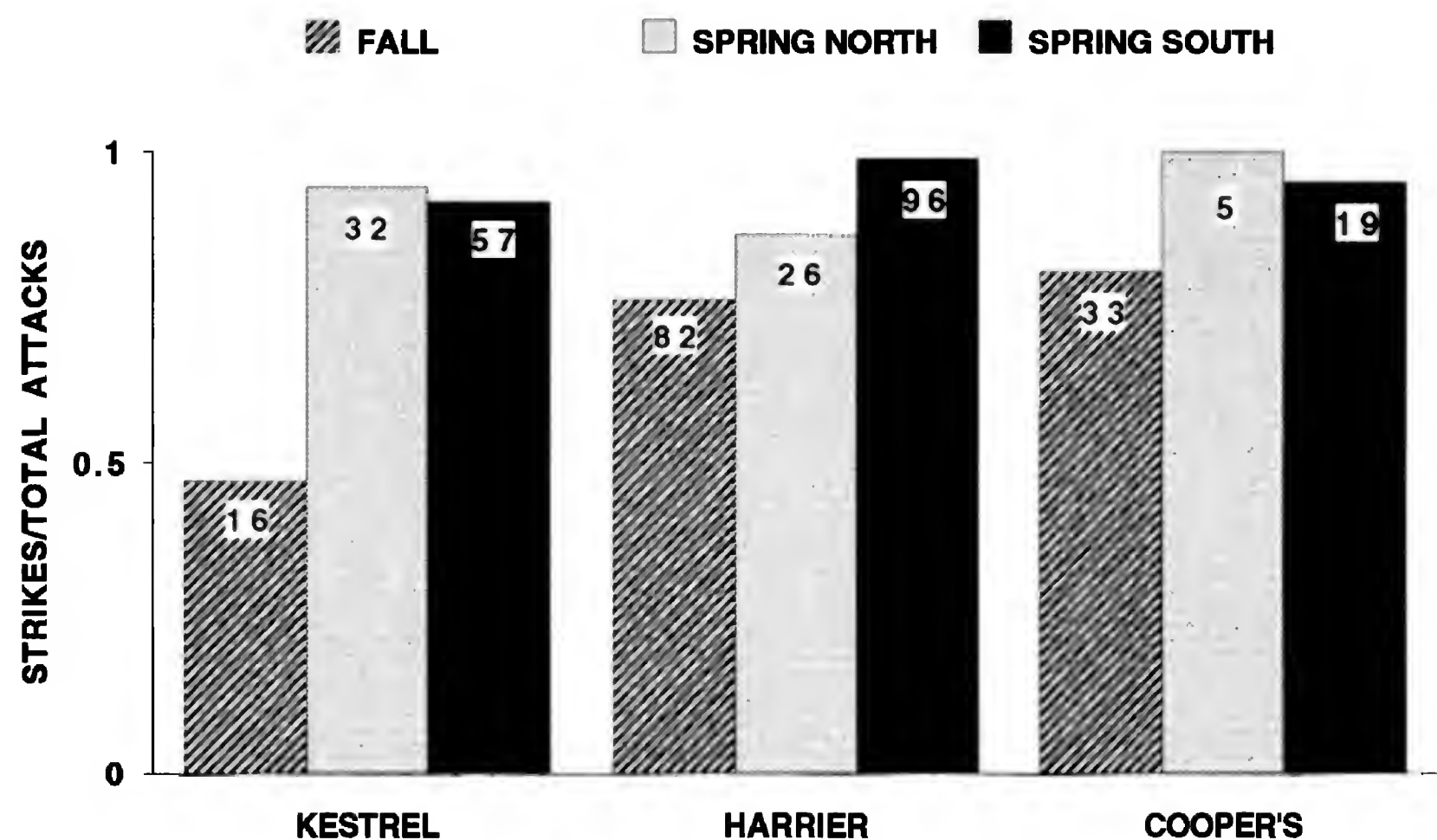
Figure 3.   Proportion of attacks that culminated in strikes instead of passes over starlings or sparrows. The numbers indicate the number of strikes. Raptors struck prey more frequently in spring than in fall (kestrels: northbound, $\chi^2 =$ 18.7, $P < 0.001$; southbound, $\chi^2 = 24.3$, $P < 0.001$. Harriers: southbound, $\chi^2 = 24$, $P < 0.001$; northbound, n.s. Most Cooper's hawks struck the lures and too few passed to permit statistical analysis).

mon raptors in fall at Cedar Grove, constituting as much as 84% of the migrants observed (Mueller and Berger 1961) but are much less common in spring, constituting less than 25% of the raptors seen. All but a few individuals of these two forest inhabiting species nest to the north of the latitude of Cedar Grove (43°40'N). Many breed to the northwest and may migrate to the southeast in fall to avoid the treeless plains, a migratory direction that would enhance their chances of encountering the western shore of Lake Michigan. A complementary migratory di-

Table 1.   Migrant Falconiformes observed and trapped at Cedar Grove, Wisconsin.

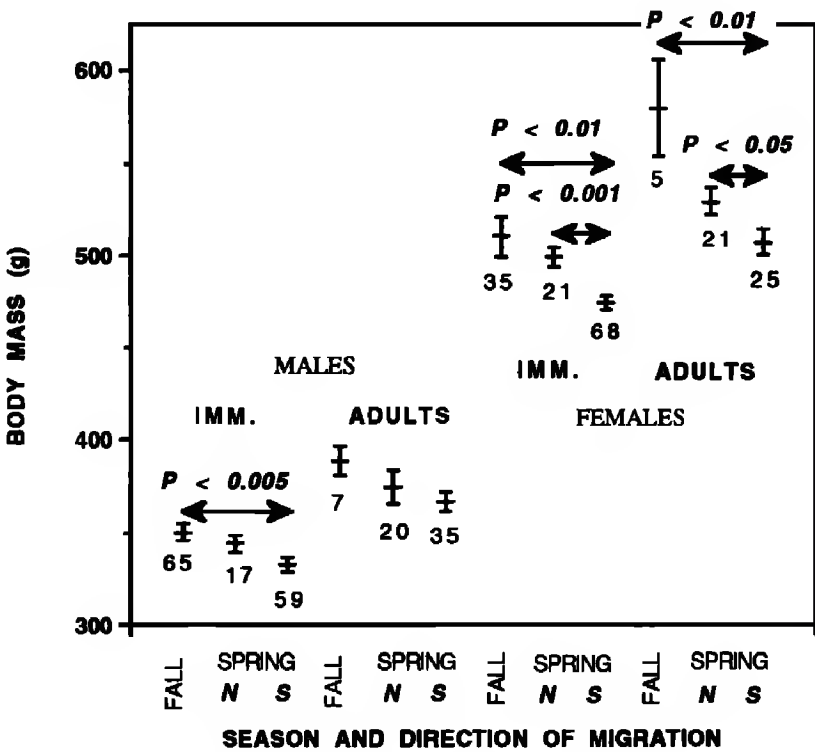|	Number Observed (% Southbound)		Number Trapped	
Species	Fall	Spring	Fall	Spring
All	48 419	9366 (40.6)	2539	851
Harrier	2042	2710 (47.9)	131	328
Cooper's	342	597 (54.9)	103	187
Kestrel	806	1453 (22.0)	42	157

Figure 4.   Body mass of Northern Harriers. The bars indicate the mean ± 1 SE. The numbers indicate the sample size. The arrows connect samples for the indicated statistical significance. Statistical differences were determined by t-test.
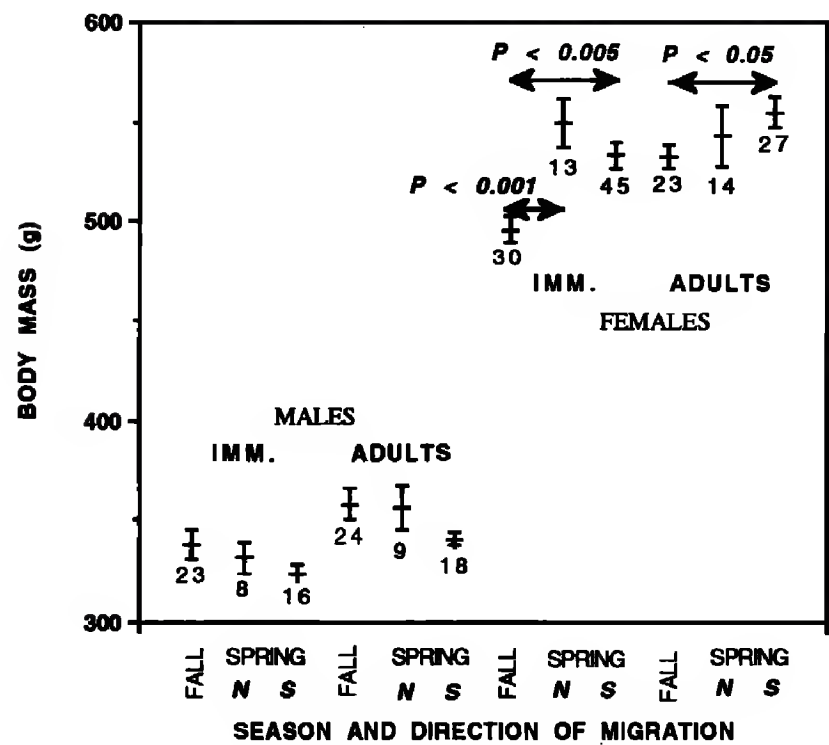
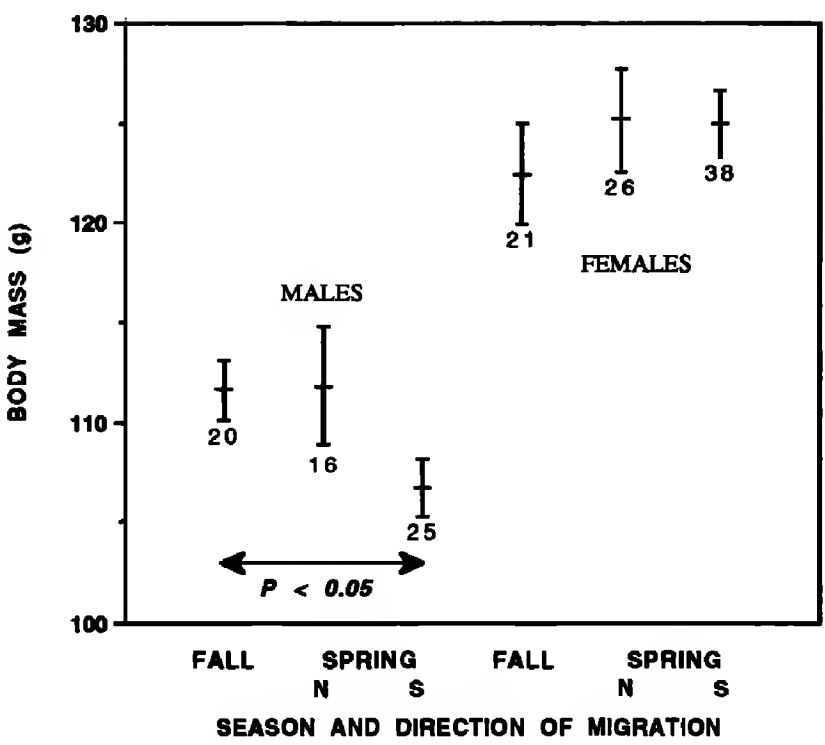Figure 5.   Body mass of Cooper's Hawks. Conventions as in Fig. 4.

Figure 6.   Body mass of American Kestrels. Conventions as in Fig. 4.

rection of northwest in spring would lead them away from the western shore.

Unlike the broad-wing and sharp-shin, Cooper's Hawks, kestrels and harriers breed commonly both

north and south of the latitude of Cedar Grove (Palmer 1988, Robbins 1991). Mueller and Berger (1969) have suggested that many of the southbound migrants at Cedar Grove in spring are birds that

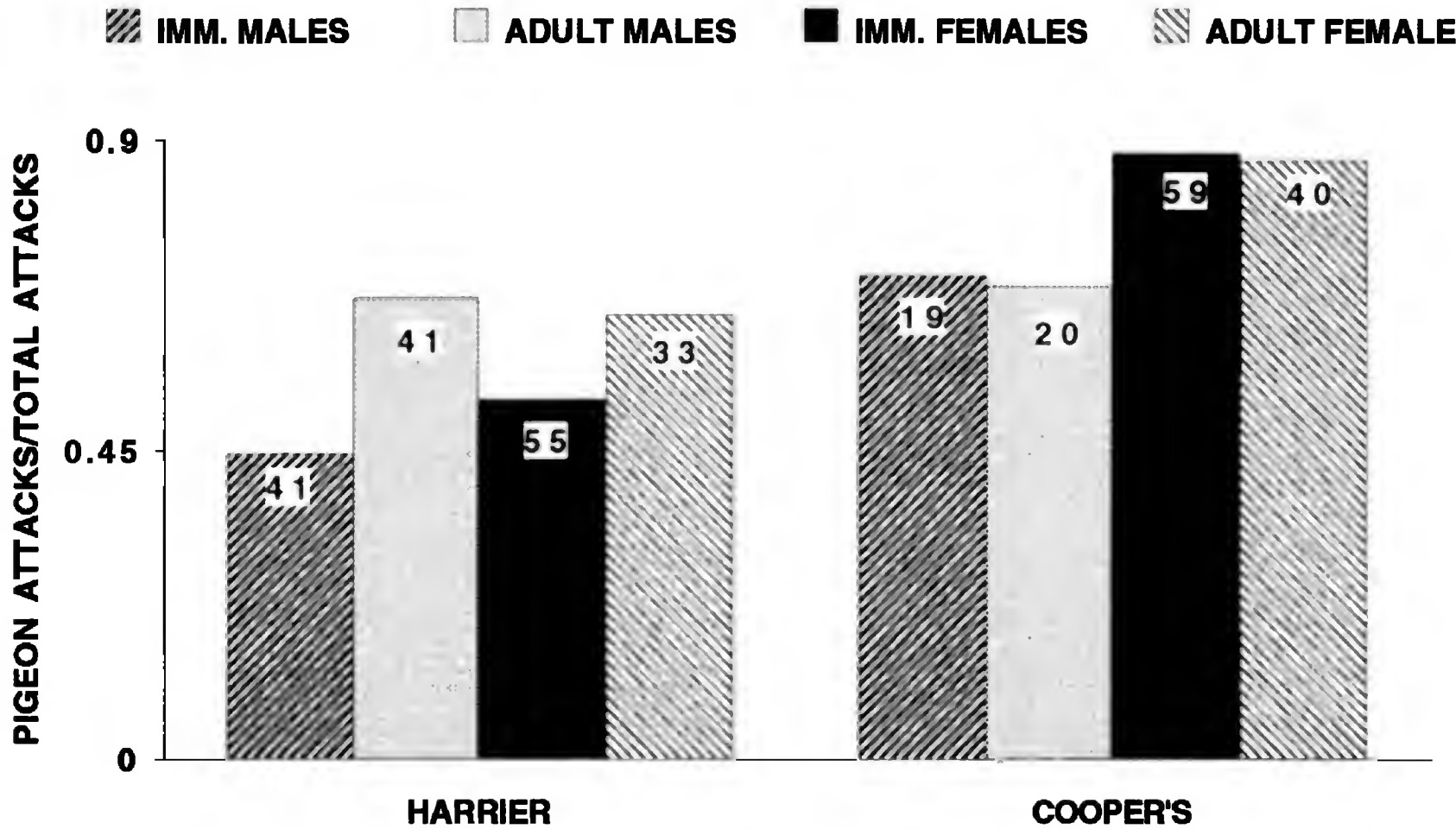Figure 7.   Attacks on pigeons as a proportion of attacks on all lure birds combined in spring. The numbers indicate the number of attacks on pigeons. Female Cooper's Hawks (adults and immatures combined) attacked pigeons more frequently than males (χ^2 = 8.86, P < 0.003). Adult Northern Harriers attacked (sexes combined) pigeons more frequently than immatures (χ^2 = 8.48, P < 0.004).
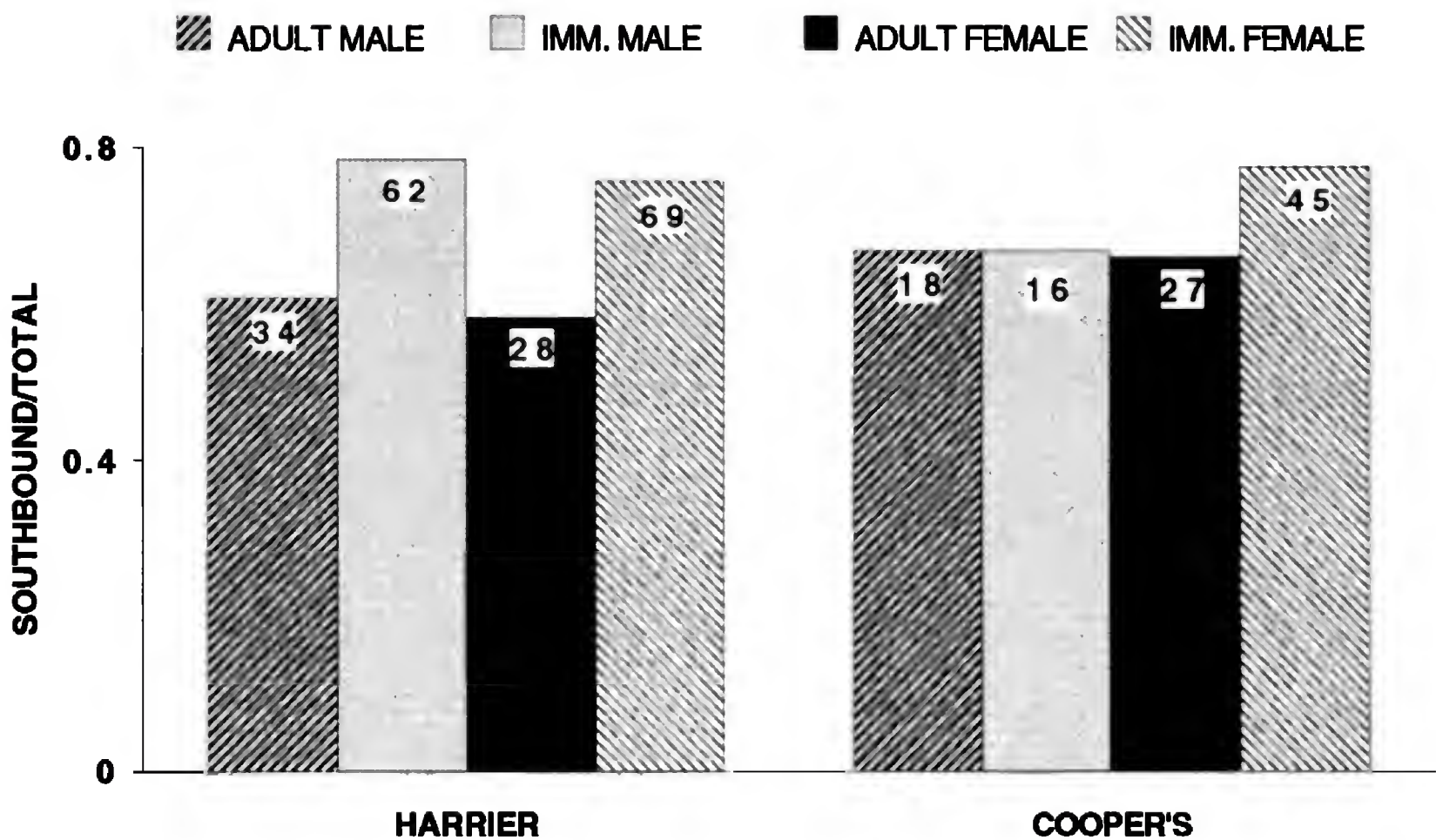
Figure 8. Southbound migrants trapped as a proportion of all spring migrants trapped. The numbers indicate the number of southbound birds trapped. More immature than adult Northern Harriers (sexes combined) were captured migrating south in spring (χ^2 = 9.43, P < 0.003).

are searching for, or reorienting, to their summer territories to the south or east of Cedar Grove after migrating too far west or north. Perhaps some of the northbound birds are reorienting to the east as well after having reached the approximate latitude of their summer home. If the navigation of hawks is as crude as Mueller and Berger (1969) have suggested, individuals of species that breed mainly to the north of Cedar Grove (such as broad-wings and sharp-shins) would still be wandering north and are less likely to be concentrated along the lake shore than reorienting individuals.

About half of the harriers and Cooper's hawks, but only one of five kestrels observed in spring are southbound (Table 1). Harriers and Cooper's hawks breed only uncommonly in the immature plumage but most kestrels breed in their first year (Meng and Rosenfield 1988, Bildstein and Gollop 1988, Henny 1972). Thus, more harriers and Cooper's hawks are non-breeders and may be wandering rather than homing to a specific breeding area, and are more likely to be southbound in spring than kestrels.

A greater proportion of the harriers captured while migrating south in spring were immatures than of

those migrating north. It is unlikely that the direction of migration affects the tendency to attack prey differently in adults and immatures; the most probable explanation is that immatures are more likely to reverse their northward migration than adults. There are no differences between the age ratios of north- and southbound Cooper's and it is not clear why the two species differ in this respect. Both breed at, and north and south of, the latitude of the station, but the Cooper's hawk is much closer to the northern limits of its breeding range than the harrier (Palmer 1988). All but a few adult Cooper's in their second year of life are embarking on their first breeding season and searching for a place to breed. Perhaps these first-time breeders are likely to migrate too far north, into areas which are only sparsely populated by the species and then reverse their direction and occur as southbound migrants at Cedar Grove. As noted previously, harriers and Cooper's hawks breed at about the same time in Wisconsin. Both species breed only uncommonly in the immature plumage, but the variance in the age ratio is higher in harriers, with more immatures breeding when vole populations are high (Hamerstrom 1988). Local popula-

tions of harriers fluctuate considerably in response to vole populations and breeding site fidelity appears to be lower in harriers than in Cooper's (cf., Hamerstrom 1986, and Moore and Henny 1984). We might thus expect young harriers to wander and search for a possible breeding locality more than Cooper's hawks. Young harriers return to their birthplace to breed less frequently than Cooper's hawks (cf., Hamerstrom 1986, Rosenfield and Bielefeldt 1992). A bird wandering eastward is more likely to pass over Cedar Grove if it turns south rather than north because of the greater effectiveness of the leading line. Immature harriers may be more likely to turn south than birds that have bred previously when they encounter the lake shore because more of them are wandering rather than attempting to return to a breeding area to the north of Cedar Grove.

In spring, southbound harriers, Cooper's and kestrels attacked our lure birds more frequently than northbound migrants. Our blind and traps are permanent structures situated, oriented and designed for the capture of southbound migrants in fall. Our lure birds must be manipulated by the trapper to be effective in attracting raptors to our traps. Northbound migrants usually are not observed from our blind until they are overhead or off to the east or west and, at best, there is very little time to operate before the birds are past and unlikely to see our lures. On some occasions we put an auxiliary observer in a small blind to the north of our traps to watch for northbound hawks and signal the trapper in the main blind. There are trees immediately to the south of our blind and the view of the auxiliary observer is far from optimal. The signaling system was also crude: variously a whistle, an electric buzzer and an old telephone. These efforts did not seem to affect the probabilities of our capturing northbound migrants consistently. Indeed, we suspect, but cannot prove, that northbound migrants would be more difficult to trap than southbound migrants even if we built a blind and traps specifically for them. Northbound migrants may be less hungry or more motivated to migrate than southbound birds. Regardless of these possibilities, the probability of capture is biased in favor of southbound birds and most comparisons between spring and fall can only be made properly among southbound birds.

In all three species, southbound migrants in spring attacked prey more frequently than fall migrants. Of the raptors attracted by our lures, more struck the lure when southbound in spring than in fall.

Cooper's and harriers attacked larger prey (pigeons) more often in spring than in fall. Three possible explanations for these seasonal changes are: 1) raptors are hungrier in spring; 2) prey are scarcer in spring, more difficult to capture and raptors must avail themselves of almost every opportunity to capture prey; and 3) the specific searching images (Tinbergen 1960, Mueller 1971, 1987) of raptors change over the winter in response to changing availabilities of prey types. These hypotheses are not mutually exclusive and there is no reason each must apply to all three species. Harriers, and particularly kestrels, may change their search image over the winter but this is clearly not the case with Cooper's hawks which prey largely on birds year-round. Hunger is also an inadequate explanation if the body mass of raptors is an unequivocal measure of appetite. Female kestrels and female Cooper's were heavier in spring than in fall (the difference is statistically significant in the latter). Yet females of both these species do not differ from males in attacking more lure birds in spring than in fall. Females may put on more fat in spring than males in preparation for breeding. This is true of the European Sparrowhawk (*A. nisus*; Newton 1986) and the Eurasian Kestrel (*F. tinnunculus*; Village 1990). A female thus might be as hungry as a male in spring even though she is fatter than the male. However, female harriers are significantly lighter, not heavier, in spring than in fall (Fig. 4), and yet they breed at approximately the same time as Cooper's and kestrels (Robbins 1991). Further inconsistencies are that male harriers and kestrels all weigh significantly less in spring than in fall and Cooper's show the same trend. Male European Sparrowhawks are heavier in spring, possibly significantly so, and Eurasian Kestrels also appear to be slightly heavier in spring than in fall. Southbound hawks of all three species attack lures more often than northbound hawks and are lighter in nine of ten comparisons and the difference is statistically significant in two cases. This nearly consistent relationship further highlights the lack of consistency in differences between fall and spring.

The remaining hypothesis, that raptors must avail themselves of opportunities of capturing prey more frequently in spring than in fall because prey is scarcer has the further virtue in being the most parsimonious of the three. Our lures are obviously attractive to raptors since we capture a reasonable proportion of the birds that we observe (Table 1, Fig. 1). One can see more attacks on birds at a hawk

trapping station in a day or two than in a lifetime of watching migrating hawks. Our lures cannot use the predator evasion tactics of immobility to avoid detection or fleeing to avoid attack. Birds that fail to use evasive tactics in the presence of a raptor must be unusual in nature and particularly rare in spring because young of the previous breeding season have had at least a half-year's experience avoiding predation and no new inexperienced young have yet appeared. Our lures should thus be more attractive in spring.

The fourfold increase in frequency of attacks on lure birds between fall and spring by kestrels can be interpreted as a switch in the specific searching image of many individuals from grasshoppers to vertebrates. On the other hand, the 1.6 fold increase in Cooper's hawks is also considerable and a change in specific searching image is not a likely explanation.

It is not surprising that female Cooper's hawks attack larger prey (pigeons) more frequently than males; females weigh about 1.5–1.6 times as much as males. However, harriers show no difference between the sexes in the frequency of attacks on pigeons even though harriers are essentially as dimorphic as Cooper's: female harriers weigh about 1.4–1.5 times as much as males (Fig. 4). Curiously, adult harriers attack pigeons more frequently than immatures but there is no such age difference in Cooper's hawks even though the age dimorphism is similar in the two species (Fig. 5, adult mass is 1.1 times that of immatures). In contrast, Mueller and Berger (1970) found that immature Sharp-shinned Hawks attacked pigeons during fall migration more frequently than adults and attributed the excessive attacks on inappropriately large prey to the relative inexperience of the young hawks. Too few harriers attack pigeons in fall for a statistical test and Fig. 7 is based on spring migrants. In spring, immature harriers have had more than 6 mo of experience but the greater experience of adults with large prey apparently is the reason adults attack pigeons more frequently. Most harriers strike the pigeons they attack (86% in fall and 99% in spring) but in 113 attacks on pigeons no sharp-shin actually struck the lure (Mueller and Berger 1970). It is unlikely that experience leads to frequent attacks on larger prey in one species and fewer in another species. We suggest that adult harriers attack pigeons more frequently than immatures because they have had successful experience with large prey. Pigeons are more than

twice as large as female sharp-shins, and more than three times as large as male sharp-shins and are clearly excessively large prey for this species. We further suggest that the attacks on pigeons by sharp-shins are not mistaken predatory attempts on inappropriately large prey, but instead are a form of play behavior. Ratcliffe (1980), Treleaven (1980), Brown (1976), and Mueller and Meyer (1985) have noted that raptors often pursue prey without intent of capture. Young mammals exhibit play behavior much more frequently than adults and we might expect the same to be true of hawks. Mueller (1974) described some play behaviors in young hand-reared kestrels; play behavior in these birds decreased with age.

The explanations offered in this paper should be regarded as suggestions for further research rather than definitive answers to the interesting questions raised by the differences in the behavior of raptors between spring and fall migration.

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RAPTOR PREDATION ON ROCK PTARMIGAN (*Lagopus mutus*) IN THE CENTRAL CANADIAN ARCTIC

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ABSTRACT.—We studied the nature and timing of raptor predation on a population of Rock Ptarmigan (*Lagopus mutus*) in the central Arctic of the Northwest Territories from 1987 to 1989. The density of Rock Ptarmigan at Windy Lake declined during the 3 years of the study from 5.8 to 3.5 to 2.8 birds per 100 ha. The number of nesting pairs of raptors within 10 km of Windy Lake also declined during this period from 9 to 10 to 5. Nesting raptors included Gyrfalcons (*Falco rusticolus*), Peregrine Falcons (*Falco peregrinus*) and Golden Eagles (*Aquila chrysaetos*). Common Ravens (*Corvus corax*) were also present. During the breeding seasons of 1988 and 1989, 15% of the adult breeding population of Rock Ptarmigan were depredated. There was no sex or age bias among Rock Ptarmigan killed, but a temporal bias was recorded over the course of the breeding season. Predation was the proximate cause of death for 91% of Rock Ptarmigan found dead over the three summers. Falcons accounted for 95% of all predation, the majority likely by Gyrfalcons.

Depredación por raptoras que victiman a las de la especie *Lagopus mutus* en el Ártico central canadiense

EXTRACTO.—Hemos estudiado la naturaleza y época de la depredación causada por raptoras en una población de *Lagopus mutus* en el Ártico central de los Territorios del Noroeste canadiense, desde 1987 a 1989. La densidad de estas raptoras en Windy Lake declinó durante los tres años de estudio desde 5.8 (1987), a 3.5 (1988), y a 2.8 (1989) aves por 100 hect. El número de parejas raptoras nidificantes dentro de 10 km de Windy Lake también declinó durante este período desde 9 (1987), a 10 (1988), a 5 (1989). Las raptoras nidificantes incluyeron especies tales como *Falco rusticolus*, *F. peregrinus*, y *Aquila chrysaetos*. Los *Corvus corax* también estuvieron presentes. Durante las estaciones de reproducción de 1988 y 1989, el 15% de la población reproductora de las *L. mutus* fue depredada. No hubo parcialidad por sexo ó edad entre las *L. mutus* que fueron muertas, pero sí se registró una parcialidad temporal durante el curso de la estación reproductora. La depredación fue la causa más probable para la muerte de 91% de *L. mutus*, a las que se las encontró muertas en el curso de tres veranos. Los halcones contribuyeron con el 95% de toda la depredación, la que, al parecer, en su mayoría fue causada por *F. rusticolus*.

[Traducción de Eudoxio Paredes-Ruiz]

In most predator-prey studies, including those of raptors and grouse, emphasis has been placed on either the predator or the prey. For example, in northern Canada, Poole (1987) studied the ecology and food habits of Gyrfalcons (*Falco rusticolus*), a major predator of ptarmigan (*Lagopus* spp.), whereas Hannon and Gruys (1987) studied the impact of predation on Willow Ptarmigan (*L. lagopus*) by mammals and raptors. Although the respective studies provided much information on the diet of Gyrfalcons (Poole and Boag 1988) and levels and patterns of predation on ptarmigan (Hannon and Gruys 1987), neither study examined the numerical relationship between predators and prey. We report on the nature and timing of predation on Rock Ptarmigan in the same area where the diet and feeding behavior of Gyrfalcons (Poole and Boag 1988) and the interrelationships within the raptor guild were reported (Poole and Bromley 1988). Our specific objectives were to determine numerically which predators were involved in ptarmigan predation, their relative impact, the relative vulnerability of different

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age and sex classes of Rock Ptarmigan, and the timing of predation relative to their annual cycle. We also examined the extent to which differences in these variables were related to seasonal and annual differences.

STUDY AREA

The study area, centered around Windy Lake, Northwest Territories (68°05′N 106°40′W), lies near the center of the Kilgavik study area used by Poole (1987) in his study of Gyrfalcons. The area consists of gently rolling tundra punctuated by small rock outcrops. The main geological features are granitic intrusions, and diabase dykes and sills (Fraser 1964). Lines of cliffs and blocks of rock rising above the surrounding terrain provide nesting ledges for Gyrfalcons, Peregrine Falcons (*Falco peregrinus*), Golden Eagles (*Aquila chrysaetos*), and Common Ravens (*Corvus corax*), the major avian predators of adult ptarmigan (Cramp and Simmons 1980, Poole 1987). For a description on the flora, fauna and climates of the region see Poole and Bromley (1988).

METHODS

We surveyed all known and potential raptor nest sites within the Kilgavik region studied by Poole and Bromley (1988) each spring (May–early June) in 1987–89 to determine occupancy status. Particular attention was given to the area within a 10 km radius of Windy Lake where, on two nearby study areas, most Rock Ptarmigan were captured and marked. Rock Ptarmigan were captured at the onset of the breeding season (early June) using a noose pole or ground nets (Hannon 1983). Sex and age were recorded for all individuals. Birds were classed as adult (≥ 1 yr old) or yearling (<1 yr old) based on the pigmentation of the eighth and ninth primaries (Parker et al. 1985). All birds were fitted with four color-coded bands: one numbered aluminum and three numbered plastic (National Band and Tag Co., Newport, KY).

In 1988 and 1989 all female Rock Ptarmigan were fitted with 12-g "necklace" radio transmitters (Biotrack, Wareham, U.K.). Only half of the males were fitted with radio transmitters; in 1988 with 18-g "backpack" radio transmitters (Telemetry Systems, U.S.A.) and in 1989 with 12-g "necklace" transmitters.

In 1987 work on ptarmigan ceased after banding was completed in mid-June. In 1988 and 1989 the fate of adult males and females was followed through to the end of each breeding season by regularly surveying (every 3–4 d) their respective territories. If an individual ptarmigan was not immediately visible, it was located by radio telemetry, or, in the case of males not radio-marked, by intensive searches of its territory.

When a ptarmigan was killed, we attempted to identify the predator from the location and nature of the ptarmigan remains. All remains were examined closely when the identity of the predator was not obvious at the kill site; a description of the location, date, and condition of the remains was recorded for comparison with descriptions in the literature for potential predator species involved (Einarsen 1956, Jenkins et al. 1964, Nielsen 1986). In some cases of presumed Gyrfalcon predation, identification was

Table 1. Number of nesting pairs of raptors within 10 km of Windy Lake, Northwest Territories, in 1987–89.

SPECIES	1987	1988	1989
Gyrfalcon	3	4	2
Peregrine Falcon	3	3	2
Golden Eagle	1	1	0
Raven[a]	2	2	1
Total	9	10	5

[a] Considered as a "functional raptor" (White and Cade 1971)

confirmed by the presence of either leg bands or radio at a nearby Gyrfalcon nest site or plucking post. Birds with transmitters that were killed by predators were found and their status documented. The fate of males without transmitters could not be ascertained in all cases, and the recorded number of males preyed upon during the breeding season is, therefore, a minimum. Predation rate was calculated as the percent of resident males or females, present at the onset of the breeding season, that were subsequently lost to predators.

Survival rates of banded ptarmigan were calculated using the Kaplan-Meier (K-M) product limit method, as modified by Pollock et al. (1989) for staggered entry of animals. Survival rates were calculated on a weekly basis. The K-M method calculates a survival function (S[t]) which is "the probability of an arbitrary animal in a population surviving t units of time from the beginning of the study" (Pollock et al. 1989). Ptarmigan, whose fate was known only up to a certain date, were eliminated from analysis from that date on (White and Garrot 1990). When dates of last observation and documented death spanned several days, a median date was used. Statistical differences in the survival function between age and sex groups were examined out using the most conservative of the three "approximate chi-square" tests presented by Pollock et al. (1989).

Data sets of observed frequencies were compared using 2 × 2 contingency analyses with the G-test of independence and Williams Correction (Sokal and Rohlf 1981). The significance level was $P < 0.05$ for all tests.

RESULTS

The number of raptors nesting within 10 km of Windy Lake declined from 1987–89 (Table 1). Falcons comprised 71% of all nesting raptors with an almost equal number of Gyrfalcons and Peregrine Falcons (Table 1). There was also a decline in ptarmigan densities per 100 ha between 1987 and 1989; from 5.8 in 1987 to 3.5 in 1988 and to 2.8 birds in 1989.

Between June 1987 and July 1989, 96% (123/128) of resident Rock Ptarmigan were marked and released, the overall sex ratio favoring males (1:0.83; Table 2). The survival function (S[t]) of these birds over the breeding season (29 May to 31 July), for
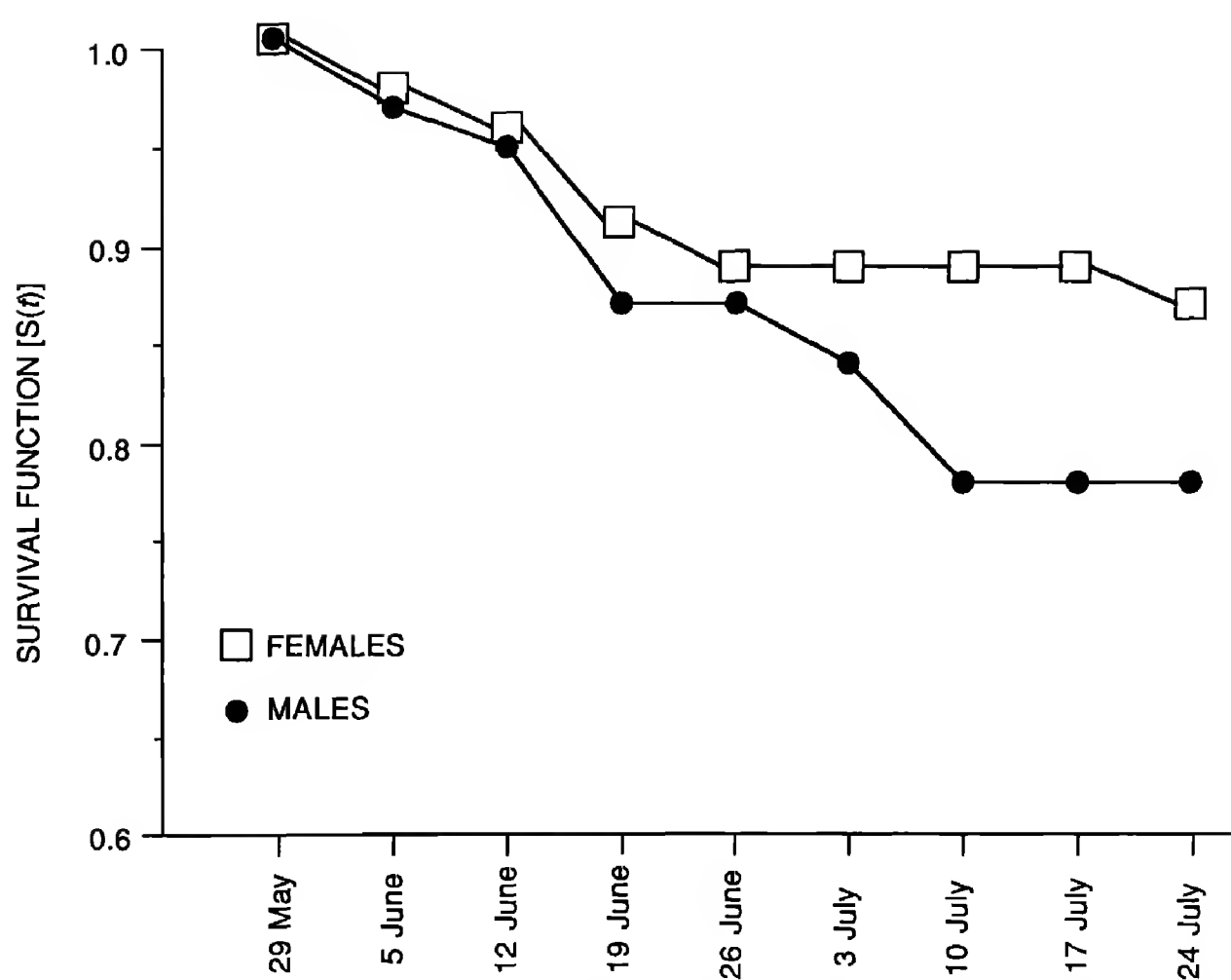
Figure 1.   The Kaplan-Meier survival function (modified for staggered entry of animals) of male and female Rock Ptarmigan over the breeding seasons of 1988 and 1989 at Windy Lake, Northwest Territories.

1988 and 1989 combined, was 0.82. There were no differences between the sexes (Fig. 1; females 0.87, males 0.78, χ^2 = 0.08, P > 0.95), or between age classes (adults 0.81, yearlings 0.84, χ^2 = 0.04, P = 0.84). Eighteen percent of birds (23/128) resident for one or more breeding seasons were found dead. Mortality over the breeding season must be considered minimal because the fate of some birds was not known at the end of the season. Assuming that all of these birds died, either during the breeding season or before returning the following spring, annual mortality would rise to 57%, somewhat higher among females (61%) than males (50%).

Predation was the proximate cause of death in 21 of 23 ptarmigan found dead over the three summers. A predator was identified for all 21 depredated Rock Ptarmigan found on the study area. All but one of the birds were killed by falcons (Table 3). The other, a female, was taken by either Red (*Vulpes vulpes*) or Arctic fox (*Alopex lagopus*). During the study, falcons killed an equal number of males (10) and females (10). Seventeen of the 21 kills occurred during the breeding season, 1 occurred in autumn, and 3 occurred between mid-summer and winter (in 1987). The predation rate during the breeding sea-

son, all years combined, was 14% (6% in 1987, 15% in 1988, and 14% in 1989). Predation rate did not differ among years (G = 0.61, df = 2, P = 0.74). Based on data from 1988 and 1989, more Rock Ptarmigan were killed in June (N = 14) than in July (N = 2) (G = 10.35, df = 1, P < 0.01). There were no differences between the proportion of males and females killed in either June (G = 0.50, P = 0.48) or July (G = 2.46, P = 0.12). A comparison of all known raptor predation events from the breeding seasons of 1988 and 1989 revealed no difference (G = 0.01, df = 2, P = 0.92) between males (15%, N = 61) and females (14%, N = 49). There was also no difference in the percentage of adults (14%, N = 63) and yearlings (14%, N = 42) killed during the breeding seasons of 1988 and 1989 (G = 0.00, P > 0.95), and this was true for both males (G = 0.24, P = 0.62) and females (G = 0.10, P = 0.75).

DISCUSSION

The density of Rock Ptarmigan at the onset of the breeding season at Windy Lake declined over the course of this 3-year study. In the larger Kilgavik region, the pattern was similar, with the decline

commencing in 1986 after 3 consecutive years of population increase (Poole and Boag 1988, Cotter 1991). The number of nesting raptors in the vicinity of Windy Lake declined from 1987–89 as well. The decline in numbers of breeding raptors, which coincided with that of the Rock Ptarmigan, suggests that these raptors assess food resources early in the season before beginning the reproductive cycle. However, Shank and Poole (1992) noted that in the larger Kilgavik region the number of productive Gyrfalcon pairs declined only slightly during those years, from 11 in 1987 to 9 in 1988, and with no change from 1988 to 1989. This discrepancy between Windy Lake and the larger Kilgavik region makes it difficult to understand whether this population of Gyrfalcons is responding to the changes in numbers of breeding ptarmigan. Court (1986) suggests that Peregrine Falcons often will hold territory early in the season but abandon it shortly thereafter and apparently forego reproduction in that year. Poole and Bromley (1988) observed among Gyrfalcons at Kilgavik that the percentage of territorial pairs to initiate laying ranged between 64 and 91%; however, regardless of the annual variation there were no differences between years in either mean brood size or productivity. The fact that those birds which did nest and produce young fledged normal numbers of chicks suggests that the precision with which food resources for breeding is measured is high.

It has been suggested that different mortality rates observed in male and female Rock Ptarmigan (Weeden and Theberge 1972) are a consequence of differences in conspicuousness of the sexes during the incubation phase of the breeding season (Bergerud and Mossop 1984). Prior to hatching, which in the Kilgavik region occurs in early July (Cotter 1991), females have been cryptic (both in plumage and behavior) for a period of 3–4 wk, whereas males have been cryptic for only a week or so (MacDonald 1970). In this study there was no sex bias in ptarmigan mortality over the course of the breeding seasons of 1988 and 1989, and this was true on a monthly basis (June and July) as well. Poole (1987) found similar proportions of each sex among prey remains taken from Gyrfalcon nest sites at Kilgavik during May–June and July–August of 1984–87. The lack of any sex bias in ptarmigan predation during the breeding season at Windy Lake and Kilgavik, particularly prior to hatching, indicates that in spite of differences in conspicuousness (and, therefore, perhaps vulnerability) of the sexes during the breeding

Table 2. Number of resident Rock Ptarmigan at the onset (approximately 1 June) of the breeding season at Windy Lake, Northwest Territories. A difference in number of males and females indicates unpaired individuals Enclosed in parentheses are percentage yearlings.

Year	Size of Study Site (ha)	Males	Fe-males	Total Density[a] (birds/ 100 ha)
1987	310	9 (33)	9 (67)	5.8
1988	1720	33 (42)	28 (46)	3.5
1989	1695	28 (7)	21 (70)	2.8

[a] 8% (10/128) of resident Rock Ptarmigan were outside of area used for calculating density.

season, falcons have equal success in taking male and female ptarmigan.

There was a temporal bias in levels of predation on Rock Ptarmigan over the course of the breeding season, with most predation having occurred in June and very little in July. There are few data from other studies on relative levels of predation during the breeding season; nevertheless, Nielsen (1986) and Poole (1987) both reported seasonal variations in the apparent vulnerability of ptarmigan to Gyrfalcon predation. Nielsen (1986) observed two seasonal peaks in vulnerability, the first during the territorial stage in the early part of the breeding season,

Table 3. Number of known depredations on male and female Rock Ptarmigan at Windy Lake, Northwest Territories, in 1987–89.

Year	Sex	Predator			
		Gyr-falcon	Pere-grine Falcon	Falcon spp.[a]	Fox spp.[b]
1987	Male	1	0	0	0
	Female	1	0	2	0
1988	Male	1	1	2	0
	Female	1	0	4	1
1989	Male	3	0	2	0
	Female	0	0	2	0

[a] Killed by either a Gyrfalcon or a Peregrine Falcon.
[b] Killed by either a Red or an Arctic fox.

and the second after the territorial system has collapsed and chicks are capable of sustained flight, commencing in late summer and lasting into early winter. The period in between coincides with a period in which ptarmigan are much more secretive and cryptic (MacDonald 1970). Poole (1987) reported a similar seasonal variation in Rock Ptarmigan use by Gyrfalcons at Kilgavik. He also observed an inverse correlation between the percentage of ptarmigan in the diet of Gyrfalcons and the availability of juvenile Arctic Ground Squirrels (*Spermophilus parryi*). At Windy Lake, juvenile ground squirrels emerged in early July (Poole 1987), and their emergence coincided with a sudden drop in the proportion of ptarmigan among the collected prey remains. Thus predation pressure on ptarmigan may reflect not only the relative vulnerability of other potential prey, but also their own behavior and crypticity. Adult male and female Rock Ptarmigan, some of which had previous breeding experience at Windy Lake, incurred losses similar to those of yearlings breeding for the first time. This suggests that any potential increased vulnerability of young birds is overcome by the time they return to the breeding grounds for the first time.

The importance of Rock Ptarmigan as prey within the arctic raptor community is evident, particularly to Gyrfalcons the range of which overlaps to a large extent the holarctic distribution of ptarmigan and the diet of which has a high percentage of ptarmigan (Bergerud and Mossop 1984, Poole and Boag 1988). At Kilgavik, adult Rock Ptarmigan are known to be preyed upon by Gyrfalcons, Peregrine Falcons and Golden Eagles, and ptarmigan remains have been found in raven nests (Poole and Bromley 1988). Although ravens may occasionally kill adult ptarmigan (Nielsen 1986), they also scavenge ptarmigan from Gyrfalcon caches (Poole and Bromley 1988). It is not surprising that Golden Eagles were not important predators as they rely on other prey for the bulk of their diet (Cramp and Simmons 1980, Poole and Bromley 1988). In the Kilgavik region, Gyrfalcons and Peregrine Falcons comprised over half the population of nesting raptors within 10 km of the Windy Lake study sites. It is, therefore, not surprising that these two falcons accounted for all Rock Ptarmigan killed by avian predators during the breeding season. It was not always possible to determine which falcon had made the kill from the remains found since both species handle prey in similar fashion (Jenkins et al. 1964, Cramp and Simmons 1980). Thus more than half the falcon kills

could not be classified to species responsible. Even so, given that seven of eight kills, for which the species of falcon was known, were by Gyrfalcons suggests that most of the falcon kills were, in fact, by Gyrfalcon. In the central Canadian Arctic, therefore, Gyrfalcons would seem to be the most important predator of Rock Ptarmigan during the breeding season (see also Bergerud and Mossop 1984, Nielsen 1986, Poole 1987, and Gardarsson 1988).

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THE EFFECT OF MAN-MADE PLATFORMS ON OSPREY REPRODUCTION AT LOON LAKE, SASKATCHEWAN

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Abstract.—Since 1975 we have banded 277 nestling Ospreys at 138 successful nests near Loon Lake, Saskatchewan. There were 137 failed nesting attempts, in total yielding a production of 277 young from 275 attempts (1.0 young per active nest). Since 1986, over half (37 of 64) of successful nests have been on man-made platforms. Pairs on platforms had a success rate of 62.9% and raised 2.1 young per successful nest, compared with a success rate of 45.9% and 2.0 young per successful nest in osprey-built nests in trees.

Alpha-numeric color bands have been added since 1988 to all nestlings and to 22 adults, including five males. Only one of the trapped adults had been banded as a nestling at Loon Lake; most others are presumed to have immigrated from elsewhere. There have been eight retrappings of six adults in subsequent years.

From 299 Loon Lake Ospreys and 14 from seven other Saskatchewan lakes, 12 recoveries to date include 2 from Colombia and 1 each from Ecuador, Panama, Costa Rica, Vera Cruz, Louisiana and New Mexico.

Efecto de las plataformas hechas por el hombre, en la reproducción de Águila Pescadora, en Loon Lake, Saskatchewan

Extracto.—Desde 1975 hemos anillado 277 Águilas Pescadoras, recién salidas de 138 nidos logrados, cerca de Loon Lake, Saskatchewan. Hubieron 137 intentos de anidar fallidos, dando en total una producción de 277 jóvenes provenientes de 275 intentos (1.0 cría por nido activo). Desde 1986, más de la mitad (37 de 64) de nidos con éxito han sido ubicados en plataformas hechas a mano. Las parejas que anidaron en estas plataformas tuvieron éxito en el 62.9% de los casos, y criaron 2.1 crías por nido logrado; comparado con el porcentaje de logros en nidos construídos en árboles por estas *Pandion haliaetus*, que fue de 45.9% y 2.0 crías por nido.

Desde 1988, anillos alfa-numerados coloreados han sido añadidos a todos los jóvenes, y a 22 adultos incluyendo cinco machos. Solo uno de los adultos atrapados ha sido anillado, como procedente de un nido de Loon Lake; la mayor parte de los otros se presume que han inmigrado de otro lugar. Seis adultos han sido racapturados ocho veces en años subsecuentes.

De 299 Águilas Pescadoras de Loon Lake, y 14 más de esta especie procedentes de otros siete lagos de Saskatchewan, hasta la fecha, 12 recuperaciones incluyen dos de Colombia y una de cada uno de los siguientes lugares: Ecuador, Panamá, Costa Rica, Veracruz, Louisiana y Nuevo México.

[Traducción de Eudoxio Paredes-Ruiz]

The association of CSH with Fran and "Hammy" Hamerstrom extends back to the meeting of the American Ornithologists' Union in Regina, Saskatchewan, in August 1959. Fran had obtained banding permits for all the states and provinces between Wisconsin and Saskatchewan. She and Hammy had cages of live pigeons and starlings on top of their station wagon and numerous sizes of bal-chatri traps. My wife, Mary, and I were entranced but our reaction paled beside that of our teenage friends and assistants, Glen Fox, Gary An- *weiler and Spencer Sealy. The boys spent a lot of time with Fran at the meeting, learning the bal-chatri technique from the expert herself. Soon after we returned to Yorkton from Regina, Gary demonstrated the effectiveness of the bal-chatri in catching kestrels in fall migration. Glen Fox in 1960 and Gary Anweiler and Ross Lein in 1961 went to Plainfield as "gabboons."*

I have been in correspondence with Fran ever since. We have met every few years at meetings of the American Ornithologists' Union or Raptor Research Foun-

dation as well as at one International Congress of Ornithology at Oxford in 1966. Without fail, we get together to discuss our recent experiences with raptors. Fran is a most encouraging person, one of the few who writes spontaneous and unsolicited compliments concerning a published paper. She was especially impressed by my owl banding efforts and shared widely with others my paper "The Year of the Owls" in 1960.

When Fran discusses a paper or asks a question at a meeting, she brings broad experience from a lifetime in the field. At the Inland Bird Banding Association at Rapid City, South Dakota, in 1987, she gave an impressive, reasoned rebuttal to counter the "pro-enforcement" video shown there concerning the raptor "sting" operation.

Mary and I have read each of her books with interest. We often read a chapter from "Walk When the Moon is Full," our favorite, to our grandchildren. Fran tells me that each one of her books has been someone's favorite, a tribute to her wide readership and the variety of topics she has written about.

The search for nests of the Osprey (*Pandion haliaetus*) in the southern edge of the boreal forest in west-central Saskatchewan began in earnest in 1975 (Scott and Surkan 1976), during weekly trips by FS by air from Loon Lake village to a clinic on the Ministikwan Indian Reserve, part of his medical practice between 1962 and 1991. This search was stimulated in part by a keen appreciation of the plight of the Osprey in his homeland, the United Kingdom. Our study of Osprey densities and productivity has caused us to make increased use of artificial platforms.

STUDY AREA AND METHODS

The area studied extends 45 km west, 15 km north and 20 km south of the village of Loon Lake (Fig. 1). Each year three aerial surveys were made, using a Piper PA 18 150 equipped with floats. The first, in May, recorded occupied nests with incubating adults. A second flight in early June identified those nests containing eggs, which were easy to see and count from the air once the adult left the nest. During a final flight in July we determined which occupied nests had been successful and attempted to assess which trees were climbable. Because the young lay flat in the nest and blended well with lining material and fish remains, they were extremely difficult to count. At all times, watch was kept for possible new nests in the forest near lakes and ponds. Most nests were within 100 m of shore and provided the occupants a view of the water, though rarely a nest was up to 2 km from water.

Over 16 years, we have spent 16 weekends in July banding nestlings, 10 weekends in March putting up nest platforms, and 3 weekends in early June trapping adults

on their nests with noose carpets. Weather has been favorable on every occasion. This effort has included a minimum of 160 hr of air time and 20 000 km by car, without counting horizontal distance by canoe, motorboat and skidoo and vertical distance climbing up 23 m trees. Up to six helpers volunteered their time and equipment on each occasion. If cost-accounted, the labor bill would be prodigious except that the work is too dangerous—no one would do it for money!

Construction of Nest Platforms. Since bulky, heavy nests at the top of dead trees are hazardous both to Ospreys and banders (in Florida, 50 to 70% of trees blew down each year; Poole 1989), we decided to construct nest platforms similar to those used in the eastern part of this continent. In Michigan, Postupalsky and Stackpole (1974) found that use of man-made platforms reduced nestling mortality from 28% to 7%, mainly by eliminating blowdowns of nest trees. In Michigan, Florida, Maryland, New York and Idaho, up to twice as many young per occupied nest were raised on platform nests as compared to tree nests (Poole 1989).

Of our first three platforms, built in March 1978, only one was close enough to allow transfer of nest material from the adjacent dead tree we pushed down by hand This platform was used that season but successfully raised young only that time, with five subsequent failures.

Platform building resumed in March 1983, when three platforms were constructed. Only the one containing Osprey nest material from a nearby dead tree was used by Ospreys. Beginning in 1984, platforms were constructed each March (1991 excepted). Since 1986 we have built each platform in a live tree next to the previously used dead tree, except in 1990, when no live tree was nearby; on this occasion we transported an 8 m high windmill frame from a deserted farm 300 km to the south and built a platform on it. Also since 1986 we have transferred most of the previous nest structure, fashioning a central cup lined with Osprey down and fish scales from the natural nest. All platforms had a frame of 5 × 15 cm lumber, supported by angle braces of the same size (Scott and Houston 1985). Attachment to the tree stump with 0.95 cm lag bolts proved inadequate as in three instances the lag bolts broke during windstorms, causing the platform to collapse. Since 1990 we have used 1.27 cm lag bolts At first we used a sheet of plywood as a base but now we use cross-planks of 5 × 10 cm lumber with gaps between allowing drainage. We were unable to collect accurate data concerning production in the 87 unsafe and unclimbable tree nest attempts.

RESULTS AND DISCUSSION

Population Density. Until 1976, only sporadic pairs of breeding Ospreys had been recorded from 44 localities in Saskatchewan (Houston et al. 1977). Since then, the Loon Lake area has supported the highest reported density of breeding pairs in Canada between the Great Lakes and the Rocky Mountains. Each year there are from 20–27 breeding pairs, for an average of one pair per 65–80 km² (Scott and Houston 1983).
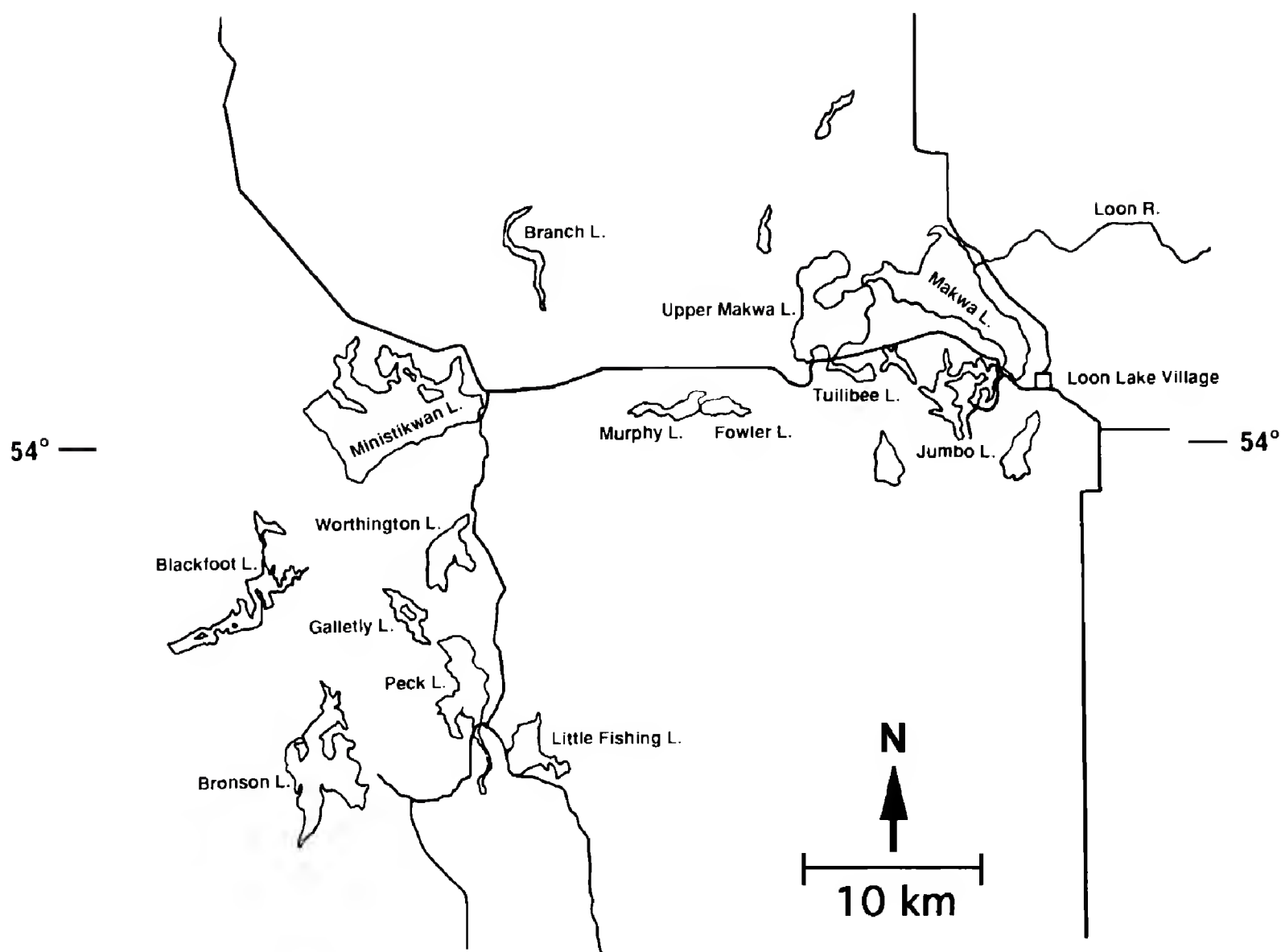
Figure 1. Map of the Loon Lake study area, Saskatchewan.

Breeding Success and Productivity. Between 1975 and 1991 there were 138 successful and 137 failed breeding attempts, producing 1.0 young per occupied nest and 2.0 young fledged per successful nest. This success was slightly lower than the 1.3 young per occupied and 2.1 per successful nest reported from Michigan (Postupalsky 1989). At Loon Lake, breeding success (Fig. 2, Table 1) varied appreciably among a) individual pairs, b) artificial nest structures and natural trees, and c) years.

Individual pairs. There were five instances of long-term breeding success and productivity far above the average; in each case Ospreys used an individual tree for many years. The two most productive nest sites were in live White Spruce (*Picea glauca*): at Branch Lake, 31 young fledged collectively in 14 of 16 yr; at Peck Lake, 21 young fledged in 12 of 17 yr. Next followed two uses of live Jackpine (*Pinus banksiana*): at Makwa Lake, where 16 young fledged in 7 of 8 yr before the tree was abandoned and at the north shore of Peck Lake, where 12 young fledged

in 6 of 10 yr of occupancy. Ten young in 6 consecutive years were fledged from a dead Jackpine at Loon River before it was replaced with a platform.

The next four most successful uses of tree sites were at Ministikwan Lake, fledging nine young in 4 of 7 yr; at Makwa Lake, with nine young in 4 of 5 yr; at Little Fishing Lake with seven young in 3 of 5 yr and Galletly Lake where seven young fledged in 3 of 5 yr.

In striking contrast, there have been 14 intermittently occupied tree sites which have produced only between one and six young during the entire study. Worse, a final 12 tree sites have produced no young, with failed attempts involving 8, 5, 4, 3, 3, 2, 1, 1, 1, 1, 1 and 1 yr, respectively. Seven of these failed sites were at the two largest lakes, five at Ministikwan Lake and two at Bronson Lake. Of 24 tree nest sites that were deserted, all had failed to produce young in the final year (in 6 instances, the only year) of occupancy.

Artificial nest platforms. As in other parts of the

Nestling Ospreys Banded at Loon Lake, Saskatchewan
Number of Nests per Year

Figure 2.   Nestling Ospreys banded at Loon Lake, Saskatchewan, 1975–91.

Table 1.   Productivity of Ospreys at Loon Lake, Saskatchewan, 1978–91.

	1975–85		1986–91		
	NUMBER ATTEMPTS	YOUNG BANDED	NUMBER ATTEMPTS	YOUNG BANDED	TOTAL ATTEMPTS
Nests not monitored					
Dead trees unsafe to climb	73	0	14	0	87
Nests monitored					
Safe trees, failed attempts	77	0	34	0	111
Platforms, failed attempts	3	0	23	0	26
Safe trees, successful	67	134	27	52	94
Platforms, successful	7	18	37	73	44
Total nests in trees	144		61		
Total nests on platforms	10		60		
Total attempts monitored	154	152	121	125	275

Figure 3.   Photograph of Osprey nest platform near Loon Lake, Saskatchewan.

continent, the prospect of a pair of Ospreys fledging one or more young was appreciably improved when artificial nest structures were used. The overall breeding success improved from 45.9% in natural trees (94 of 205 attempts) to 62.9% on man-made platforms (44 of 70 attempts). This difference is statistically significant (χ^2 = 6.035, P < 0.025).

We learned from experience. Our first ten platforms received only 33% occupancy, whereas the last ten platforms have achieved 95% occupancy (22 platform-years with success, 16 platform-years with failures and only 2 yr where a platform was not used; Table 2, Fig. 3). For these reasons we have chosen to emphasize the difference between the data sets from 1978 through 1985 and the recent years, 1986–91.

An overall average of 1.3 young were fledged per platform breeding attempt (91/70) as compared to 0.9 young fledged per tree nest breeding attempt (186/205). However, if one excludes failed attempts, the two nest site categories are not significantly different: 2.1 per young per successful platform nest

(91/44) and 2.0 per young per successful tree nest (186/94).

At this latitude (54°N), we have not yet observed building of a new nest and successful production of young in the same year. Though building of a new nest was sometimes initiated after the original nest blew down, completion was always too late for young to be produced that season. Therefore, a nest platform has the potential to save 2 yr of production: the year the nest would have blown down and the year a new nest would be built.

Since 1986 we have left few unsafe nest trees standing and have replaced them with platforms. While 67 of 74 successful breeding attempts in the first 11 yr were in trees and only 7 on platforms, in the last 6 yr over half of the successful nest attempts, 37 of the last 64, have been on platforms.

Year. Poor overall success may be related in part to inclement weather. In 1990, the year of lowest production, after a storm on 3 July with moderate winds, cool temperatures (7°C), and steady rain (43 mm), there was marked brood reduction by 14–15

Table 2.   Osprey nest platforms built at Loon Lake, 1978–90, and used through 1991.

YEAR BUILT	YEARS WITH SUCCESS	YEARS WITH FAILURE	YEARS NOT USED	COMMENTS
1978 #1	1	5	8	
#2	0	0	14	
#3	0	0	14	
1983 #4	4	2	2	Ospreys built 2× in nearby dead trees
#5	0	0	9	
#6	0	0	9	
1984 #7	3	0	5	
#8	4	0	4	
1985 #9	6	1	0	Lag bolts broke 1991
#10	4	2	1	Lag bolts replaced spring 1989 Ospreys built in dead tree 1991
First ten total	22	10	66	First ten platforms 32/98 or 33% usage
1986 #11	3	3	0	
#12	2	3	1	
1987 #13	3	2	0	
#14	4	1	0	One with addled eggs 1990
1988 #15	2	1	1	
#16	3	1	0	Lag bolts broke 1990
1989 #17	0	3	0	One with addled eggs 1991
#18	2	1	0	
1990 #19	2	0	0	Platform on 1st windmill frame
#20	1	1	0	Headless yg in nest 1990
Second ten total	22	16	2	Last ten platforms since 1986 38/40 or 95% usage
Total	44	26	68	

July, possibly as a result of exposure. With favorable weather in 1991, more young Ospreys were produced than ever before, even though there were fewer nesting attempts. We have not discerned any relation with food supply as measured by human fishing success on adjacent lakes.

Trapping of Adults with Noose Carpets. Since ours is the most discrete population recorded in Saskatchewan, we hoped that trapping of adults on the nest, in 1988–90, would result in recapture of Ospreys banded in the area as nestlings.

The one adult that had been raised and later was trapped locally was 608-09790, banded as a nestling on 18 July 1976 at Branch Lake. This bird was trapped as an adult female on her nest on 3 June 1989 at Makwa Lake and again at the same nest on 2 June 1990. She was incubating three eggs each time, 6 km south and 18 km east of where she had been banded as a nestling.

Re-trapped banded adults were as follows: in 1989, three females banded as adults on nest in 1988; in 1990, two females banded as adults in 1988, two females banded as adults in 1989 and one male banded as an adult in 1989. Only one female had shifted to a different nest site.

We watched carefully for any adverse effects of trapping but observed none in the first 2 yr. In 1988, from 11 adult capture attempts we trapped 7 adults at six platforms and one tree. The tree nest fell down, but five of six platforms were successful and fledged 12 young. In 1989, 13 of 15 attempts were successful; we caught 13 adults, 9 of which were unbanded, at 11 platforms (both adults at one) and 1 tree; 8 of the 11 platforms were successful and fledged 18 young and the tree nest fledged 1 young.

In 1990, in 12 of 14 attempts we caught 12 adults (6 unbanded) at 11 platforms; 7 platforms failed and the other 4 raised only six young. Although we were

concerned that our trapping might have contributed to this poor result, it was more likely a part of the generalized poor productivity that year, for at the seven tree nests, where no trapping of adults had been attempted, five failed and the two successful tree nests fledged only one young each.

A single banded Osprey among 23 adults trapped on the nest (7 new adults nest-trapped in 1988, 9 new adults in 1989 and 6 new adults in 1990) may be an indication that there is a wider dispersal of Ospreys in Saskatchewan than among eastern populations (cf., Postupalsky 1989).

In case our trapping intervention had contributed in part to the decreased nest success in 1990, we avoided trapping of adults in 1991. We plan to resume trapping adults in odd-numbered years only.

Migration. From 277 nestling Loon Lake Ospreys and 14 from seven other Saskatchewan lakes, 12 recoveries to date include 2 from Colombia and 1 each from Ecuador, Panama, Costa Rica, Veracruz, Louisiana and New Mexico. As yet there have been no distant recoveries from the 22 adults banded (Ewins and Houston in press).

"Leapfrogging," whereby the most northerly birds winter farther south, appears to occur in western North America, though the sample size is yet small. Ospreys from Saskatchewan and British Columbia winter in southern Central America and in northwestern South America as far south as the equator, farther south than the main wintering area (Mexico) of western United States birds (Poole and Agler 1987).

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A 24-YEAR STUDY OF BALD EAGLES ON BESNARD LAKE, SASKATCHEWAN

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Abstract.—Productivity of Bald Eagles (*Haliaeetus leucocephalus*) on Besnard Lake over a 24-year period was relatively stable. Occasional decreases in productivity appear related to weather conditions encountered during spring migration and upon arrival at Besnard Lake. Studies of four marked birds suggest considerable nest site fidelity. Observations of marked eagles in combination with surveys of Bald Eagles on Besnard and other local lakes provide insight into age structure for the local population and into adult mortality rates. We estimate adult mortality in this stable population to be 6.5–7.7%. Population stability appears to be maintained as a result of the eagles' deferring first breeding to age six.

Veinticuatro años de estudios sobre el Águila Cabeciblanca en el Lago Besnard, Saskatchewan

Extracto.—La reproducción del Águila Cabeciblanca (*Haliaeetus leucocephalus*) en el Lago Besnard, en un período de 24 años, ha sido relativamente estable. Un decrecimiento ocasional en la reproducción parece estar relacionado con las condiciones climatológicas que encuentran estas aves en sus migraciones de primavera y a su llegada al área del Lago Besnard. Estudios hechos con cuatro aves marcadas sugieren una considerable fidelidad al sitio de ubicación del nido. Observaciones sobre águilas marcadas, en combinación con conteos poblacionales de esta especie en el Lago Besnard y otros lagos locales, dan una percepción clara tanto de la distribución por edades de la población local como de la proporción en la mortalidad de adultos. En esta población estable, estimamos que la mortalidad en los adultos es de 6.5% a 7.7%. La estabilidad poblacional parece mantenerse por el hecho de que estas águilas difieren, hasta la edad de seis años, el primer ciclo reproductivo.

[Traducción de Eudoxio Paredes-Ruiz]

*It seems fitting to honor the Hamerstroms by reporting results of a long-term study of a raptor population. Both Frederick and Frances Hamerstrom were keenly interested in raptors and other birds and, as a team, they combined long-term studies first of Greater Prairie Chickens (*Tympanuchus cupido*) and, later, of Northern Harriers (*Circus cyaneus*; Hamerstrom 1986).*

Our focus has been a population of Bald Eagles (*Haliaeetus leucocephalus*) on Besnard Lake in northern Saskatchewan. Studies reported here occurred coincident with considerable concern about the effects of DDT on eagle populations in North America. In this respect, our studies parallel those of Frances Hamerstrom's on the Northern Harrier. However, the harriers studied by Hamerstrom were severely affected by DDT; the Bald Eagles in north-ern Saskatchewan were sufficiently isolated to escape appreciable detrimental effects due to the pesticide (Whitfield et al. 1974). Furthermore, fish, the primary food of Bald Eagles at Besnard Lake, form a stable prey base and our studies have revealed a relatively stable Bald Eagle population. In contrast, the voles eaten by harriers fluctuate dramatically in numbers (Hamerstrom 1986) as a result of DDT or the shifting availability of food. Our studies have provided evidence for nest and mate fidelity and provide insight into the regulation and limitation of Bald Eagle numbers in a stable population.

Study Area

Besnard Lake, situated along the southern boundary of the Canadian Shield in northern Saskatchewan, has an irregular outline with rocky shores and numerous (255) islands. Its water area is 160 km² and its shoreline is 400
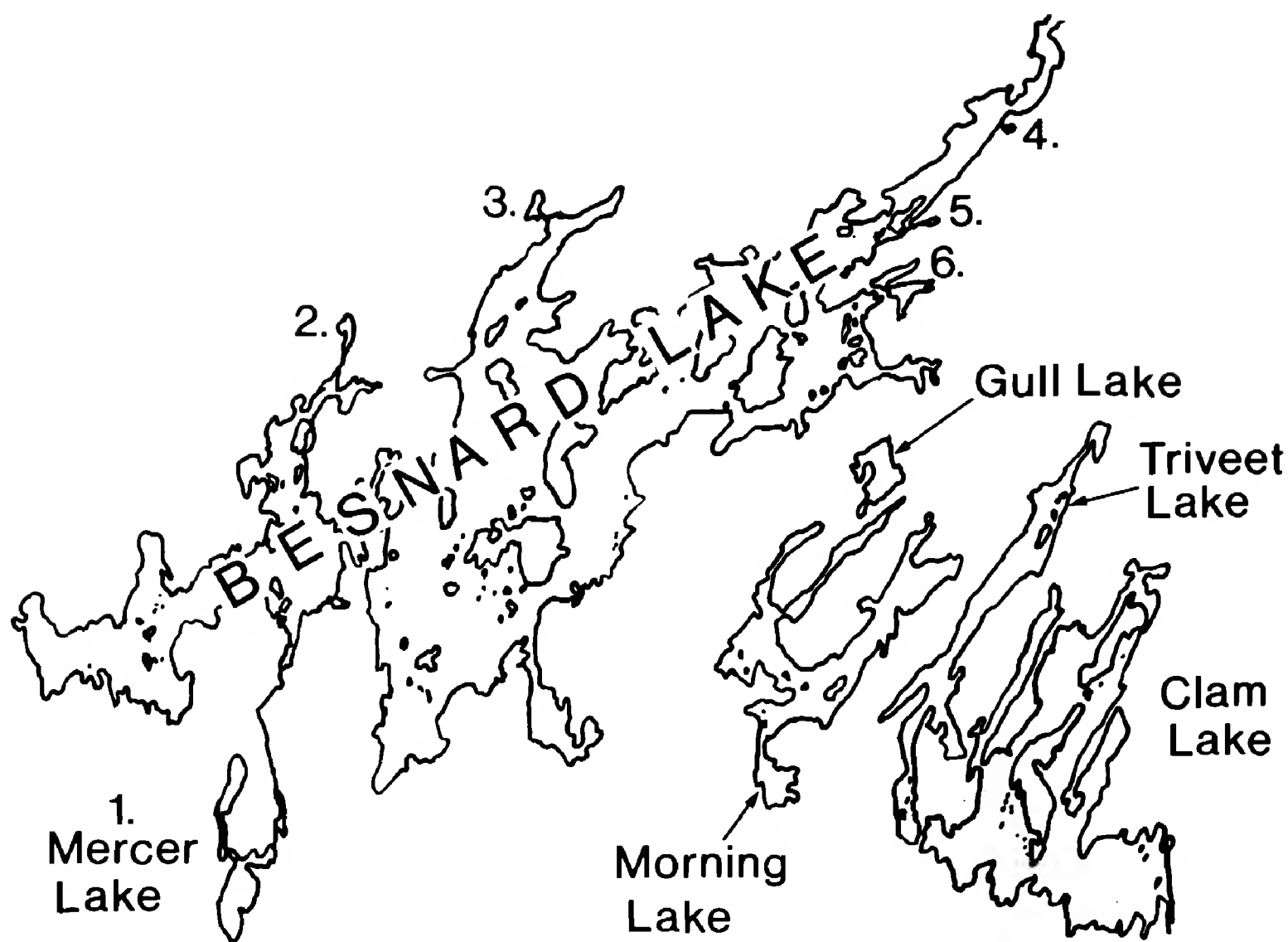
Figure 1.   The study area, including Besnard Lake. Those small lakes adjacent to Besnard Lake where streams used for spawning enter Besnard Lake and where immature eagles congregate during May and June are numbered 1–6. Also shown are the lakes of intermediate size: Gull, Morning, Triveet, and Clam lakes.

km in length. It is surrounded by low forested hills not exceeding 100 m in height. White Spruce (*Picea glauca*) and Trembling Aspen (*Populus tremuloides*) predominate near the lake shore. The lake is divided into eastern (75% of the lake area) and western (25% of the lake area) regions, connected only by an 8 meter-wide narrows. The mean depth of Besnard Lake is 7.9 m, giving the lake a water volume of 1.4×10^9 m^3. The maximum depth is 26.8 m. Additional details of the geography, morphology, and biological features are given in Chen et al. (1974).

Besnard Lake freezes over to a depth of up to 2.2 m in the winter. Ice break-up is usually in mid-May. Bald Eagles return at the end of March or in early April and remain as late as freeze-up, which is usually in mid- to late November. Migratory patterns of Besnard Lake Bald Eagles have been described elsewhere (Gerrard et al. 1978). The study area also includes six small lakes at 0.4–3.7 km^2 water area near Besnard Lake (Numbers 1–6, Fig. 1). The character of the shores and forests surrounding these lakes is similar to Besnard Lake, except that one small lake (Mercer Lake) has extensive shallow, reedy areas.

Four intermediate sized lakes (Gull, Morning, Triveet, and Clam), as shown in Figure 1, were included for certain

studies. These lakes are near to Besnard Lake and similar to Besnard and are located along the southern boundary of the Canadian Shield region (Gerrard and Gerrard 1985, Dzus and Gerrard 1989). As with Besnard Lake, these lakes have irregular outlines with rocky shores and numerous islands. The total shoreline of all four lakes is 360 km^2, slightly less than the total shoreline of Besnard Lake. The terrain is similar to Besnard Lake, although Morning Lake is distinctive in having several large bays with substantial amounts of wild rice.

METHODS

Bald Eagle productivity on Besnard Lake has been checked annually since 1968. Status of nests was usually evaluated as recommended by Postupalsky (1974) during incubation in April or May, and then at intervals during June, July and August. Aerial censuses were performed in July 1968, May 1969, July 1969, April 1970, April 1973, May 1974, April 1986 and May 1987. All other censuses were conducted by boat, as previously described (Gerrard et al. 1990) with one or more observers travelling 100 m from the shore in a motorboat at a speed of 8–16 km/hr covering alternate 8 km sections of lake shoreline with half the lake (25 sections) covered in a survey. Ob-

Table 1. Breeding areas and reproductive indices for Bald Eagles at Besnard Lake, Saskatchewan (1968-91).

			Number of		
Year	Breeding Areas	Percentage of Successful Breeding Areas[b]	Young per Occupied Breeding Area	Young per Successful Breeding Area	Young Fledged
1968[a]	8	83	1.33-1.5	1.6-1.8	8-9
1969[a]	16	67	1.0-1.2	1.5-1.8	15-18
1970[a]	16	75	1.25	1.67	20
1971[a]	15	53-80	1.0-1.5	1.88	15
1972[a]	16	75-80	1.06-1.13	1.42	17
1973	25	68	0.88-0.96	1.3-1.44	22-24
1974	25	65	0.96	1.47	22
1975	25	46-61	0.63-0.83	1.36	15
1976	25	67	1.14	1.71	24
1977	24	78-82	1.26-1.32	1.61	29
1978	25	74	1.17-1.22	1.59-1.64	27-28
1979	24	79	1.26	1.60	24
1980	24	74-77	1.22-1.27	1.65	28
1981	24	67	1.19	1.79	25
1982	24	81	1.38	1.71	29
1983	24	83	1.56	1.67	25
1984	25-26	72-75	1.35	1.72	31
1985	28	58	0.95	1.64	23
1986	31-36	50-58	0.75-0.87	1.50	21
1987	29	70	1.11	1.58	30
1988	29	66	1.22	1.74	33
1989	25-26	77-80	1.23-1.28	1.60	32
1990	29	56	0.81	1.47	22
1991	28	52-54	0.92-0.96	1.77	23

[a] Coverage was possibly incomplete.
[b] Successful breeding areas/occupied breeding areas.

servers were on the lake for 1-5 mo in all years except 1971, when a single boat census was conducted in July, and in 1983, 1985, 1989, 1990 and 1991 when the observation period was restricted to 2-3 wk in July.

We have used the following terms (Gerrard et al. 1983). A breeding area refers to one or more Bald Eagle nests within the range of a mated pair. An occupied breeding area is one with a mated pair consistently using the area that year. An active breeding area represents one in which at least one egg was laid. A successful breeding area is one where one or more young were raised to fledging.

Red, yellow, and green patagial tags were used to mark 56 nestling eagles on Besnard Lake from 1973-75 (Gerrard et al. 1978). Two nesting adults were captured as described by Harmata (1985) and marked using colored and numbered leg bands, one in 1988 and one in 1989. Age and sex of nestling Bald Eagles were determined using criteria described by Bortolotti (1984).

RESULTS

Table 1 provides the number of breeding areas and several reproductive indices for Bald Eagles on Besnard Lake, 1968-91. Number of young raised per occupied breeding area has varied through the years 1968-91. The years 1973-75, 1985-86, 1990-91 showed values of less than one young produced per occupied breeding area. There was a particularly sharp decrease in productivity in 1975.

Population Stability. Fifty-three ± 1.1 ($\bar{x}$ ± SE) Bald Eagles were seen on six surveys in July 1976-79, giving an estimated lake population (nestlings excluded) of 106 eagles. Forty-nine and 54 Bald Eagles were seen on six surveys in July 1990, for an estimated lake population of 103 eagles.

Nest Site and Mate Fidelity. A female hatched on Besnard Lake in 1973 occupied nest Y with a mate in 1979 at age 6, and bred successfully from 1980-91, with the exception of 1990 (Table 2). A female hatched on Besnard Lake in 1974 was first observed at nest M in 1984 and has bred successfully

Table 2. Sightings of nesting adults marked as nestlings or adults on the Besnard Lake study area and their subsequent nesting success, 1979–91.

	YOUNG FLEDGED BY MARKED EAGLES			
YEAR	Y (FEMALE)	M (FEMALE)	O (MALE)	T (FEMALE)
1979	0			
1980	2			
1981	2			
1982	2			
1983	2			
1984	2	2		
1985	1	not seen		
1986	2	1		
1987	2	2	2	
1988	3	2	2	2
1989	2	2	2	2
1990	0	0	not seen	0
1991	3	2	not seen	0

on this territory for six of eight years from 1984–91. A male hatched on Besnard Lake in 1980 bred for three successive years during 1987–89 at nest Θ. A female captured as an adult at nest T in 1988 bred in 1988 and 1989 and has continued in the same territory with a mate in 1990 and 1991. Additional data suggest that unmarked females repeatedly used the same breeding area. There was a significant correlation (r = 0.907, df = 4, $P < 0.05$) between the lengths of eggs collected at the same nest in two different years (order in the laying sequence within the clutch was held constant between years). Variation in egg length among nests was three times greater than variation within nests compared among years. Behavior of pairs (e.g., tame or aggressive in response to investigators climbing their nest trees) was consistent throughout 1980–82; there was a very high correlation between the aggressiveness in nest defense score between two consecutive years (r = 0.955, df = 6, $P < 0.01$). Each breeding area was represented only once in the latter analysis to maintain the independence of samples. Breeding areas with young in all three years were consistent in the aggressiveness of attending pairs (e.g., the mean scores for the three years for three nests were 1.9, 1.8, 2.0, and 4.4, 4.9, 4.8, and 3.6, 3.6, 3.8). We noticed consistencies in the behavior of many pairs for several years before we quantified nest defence.

Overall Population Composition. Using data from boat censuses of Besnard Lake (Gerrard et al. 1990) and adjacent small and intermediate-sized lakes (Dzus and Gerrard 1989) we estimated the proportion of Bald Eagles in different age categories for this area for May and June and for July and August (Table 3). Of all eagles (nestlings included), 25–30% were adults at active nests, 4–5% were adults at inactive or failed nests, 13–19% were adults not associated with nests, and 30–33% were immatures. The nestlings raised on Besnard Lake made up 18–22% of the population at the end of the summer. Information on the age and composition of a population can be used to estimate survival rates for immatures and adults (Sherrod et al. 1976). Knowing that the Besnard Lake eagle population has been stable for many years, and using the data in Table 3, we calculated mortality rates for eagles in the Besnard Lake population. Based on studies of color marked eagles (three color marked adults seen at age four were not breeding; three color marked birds seen at age five were not breeding; one color marked bird occupied a breeding territory at age six and successfully raised young for the first time at age seven), we estimate that adult eagles at Besnard Lake enter the breeding population at the average age of six. In a stable population, adult mortality must equal recruitment into the breeding populations. Given a population (Table 3) with nestlings comprising 20–21% of the population, 1–3 year olds comprising 31–32%, 4 and 5 year olds comprising 17–19%, and eagles 6 or more years old comprising 30–33%, the maximum yearly adult mortality can be no greater than 7.7% (Table 4). If Bald Eagle mortality declined over the first few years (Table 5), then adult mortality could be as low as 6.5%. It should be noted that even if Bald Eagles bred at age 4, adult mortality would only increase to 8.8% (Table 6).

DISCUSSION

Results of the study on Besnard Lake give insight into population dynamics of a stable Bald Eagle population. Before 1973, some nests may have been overlooked. However, aerial censuses were conducted in Spring 1969 and in April 1970. Furthermore, observers were on the lake for 6 wk in 1970 and for the full summer of 1972. Thus, while we are cautious in saying that there may have been nests missed in the early years, these were probably few, and some increase in the number of breeding eagles

Table 3. The number and percentage of Bald Eagles for A) all May and June censuses and the mean number of each category of eagles seen on Besnard Lake, the intermediate lakes and the small lakes; B) the July and August censuses for Besnard Lake, the intermediate lakes and the small lakes, and C) all July and August censuses of Besnard Lake only.

				PERCENT OF		
		NUMBER OF EAGLES	ADULTS	EAGLES (NESTLINGS EXCLUDED)	ALL EAGLES (NESTLINGS INCLUDED)
I. Adults at nests where eggs were laid	A) May/June (study area)	60.5	51.7	30.6	25.0
	B) July/August (study area)	61.5	62.8	38.3	29.9
	C) July/August (Besnard Lake)	37.5	61.9	37.8	29.6
II. Adults at nests where no eggs were laid	A) May/June (study area)	9.7	8.3	4.9	4.0
	B) July/August (study area)	8.5	8.7	5.3	4.1
	C) July/August (Besnard Lake)	6.5	10.7	6.5	5.1
III. Adults not associated with nests	A) May/June (study area)	46.75	40.0	23.6	19.3
	B) July/August (study area)	28.0	28.6	17.5	13.6
	C) July/August (Besnard Lake)	16.6	27.4	16.7	13.3
IV. Immatures (Aged 1–3 yr)	A) May/June (study area)	81.0	—	40.9	33.4
	B) July/August (study area)	62.4	—	38.9	30.4
	C) July/August (Besnard Lake)	38.7	—	39.0	30.5
V. Nestlings	A) May/June (study area)	44.4	—	—	18.3
	B) July/August (study area)	45.0	—	—	21.9
	C) July/August (Besnard Lake)	27.5	—	—	21.7

likely occurred from 1969–73. Further, the number of occupied breeding areas from 1984–91 was, in general, slightly higher than the number from 1973–83. Thus, there has been a modest increase in the number of breeding adults on Besnard Lake during the years of the study. Boat censuses designed to

evaluate the overall population (Gerrard et al. 1990) suggest that the total number of Bald Eagles using Besnard Lake has not changed from 1976–90.

Primary prey utilized by this population was fish, a prey base which for Besnard Lake has been relatively stable. There has been increased fishing pressure and a noticeable decrease in the size of walleye (*Stizostedion vitreum*) caught by fishermen (J.M.G.

Table 4. Estimate of Bald Eagle mortality rates at Besnard Lake assuming mortality constant after year one and age at first breeding = 6.

AGE CLASS	PERCENTAGE OF POPULATION	MORTALITY
Fledglings	20.10%	43%
1 year old	11.50%	7.7%
2 years old	10.61%	7.7%
3 years old	9.80%	7.7%
4 years old	9.04%	7.7%
5 years old	8.34%	7.7%
6 years old	7.70%	7.7%
7 or more years old	22.91%	7.7%

Table 5. Estimate of Bald Eagle survival with mortality decreasing until age 6 and age at first breeding = 6.

AGE CLASS	PERCENT OF POPULATION	MORTALITY
Fledglings	20.10%	36%
1 year old	12.86%	20%
2 years old	10.79%	15%
3 years old	8.74%	11%
4 years old	7.78%	9%
5 years old	7.08%	7.5%
6 years old	6.55%	6.5%
7 or more years old	26.60%	6.5%

Table 6. Maximum estimate of adult Bald Eagle mortality rate assuming mortality constant after year one and age at first breeding = 4.

AGE CLASS	PERCENT OF POPULATION	MORTALITY
Fledglings	20.10%	42%
1 year old	11.65%	8.8%
2 years old	10.62%	8.8%
3 years old	9.69%	8.8%
4 years old	8.84%	8.8%
5 or more years old	39.10%	8.8%

personal observations), and a decrease in the number of the largest sizes of northern pike (*Exos lucius*). It is possible that fish such as cisco (*Coregonus artedis*) may have increased with fewer predatory walleye and pike. Bald Eagles preferentially feed on cisco (Gerrard and Bortolotti 1988) and numbers of Bald Eagles on Besnard and Nemeiben lakes have been related to number of cisco in these two lakes (Dzus 1988). A modest increase in cisco from 1973–91 is one potential explanation for a modest increase in breeding eagles.

Association of poor productivity in Bald Eagles with weather conditions in spring is consistent with data from other areas, suggesting that spring conditions may limit breeding success (Leighton et al. 1979, Swenson et al. 1986). In 1975 a series of severe snowstorms swept across northern Saskatchewan during eagle migration, severely disrupting their return to the nesting grounds (Gerrard and Whitfield 1979). We suspect that females arrived back in poor shape and bred much less successfully than usual. The decrease in young raised on Besnard Lake in 1975 was reflected over a fairly wide area of northern Saskatchewan and perhaps adjacent Manitoba, Alberta, and the Northwest Territories. There was a significant decrease in the number of immature eagles seen on the wintering grounds on the Christmas bird counts in 1975–77, consistent with the observed decrease in productivity in 1975 (Gerrard and Whitfield 1979). Although analyzed in much less detail, 1990 appears to have been similar to 1975. At the time that eagles return, the lake is usually still frozen and fish or other prey may be difficult to find. This is a time when food is limited and it is likely that the condition of adults based on their winter feeding pattern (Harmata 1984), their experience during

migration, and in the first few days at Besnard Lake has a significant influence on breeding success.

Observations of four color marked eagles show considerable nest site fidelity and imply, therefore, a degree of mate fidelity. In addition to our observations of marked eagles, evidence from egg measurements and from observations of behavior supports the concept that the same pairs inhabited the same breeding areas year after year. A further example of nest fidelity was a female, identifiable by unique plumage, which was an occupant of one breeding area from at least 1979–81 (Bortolotti and Honeyman 1985). Taken together, these observations suggest strong nest site and mate fidelity in this population of Bald Eagles.

Estimating the age structure of the Bald Eagle population is difficult when there has been some movement on and off Besnard. The May/June data for Besnard Lake alone, or for the intermediate-sized lakes alone show that the various age classes were unevenly distributed within the study area, with the immatures and non-breeding adults gathering at spawning streams and small lakes with winter kill of fish during May and June (Gerrard et al. 1990). Combining estimates of numbers of eagles in May and June on Besnard Lake with numbers from adjacent intermediate and small lakes is necessary to give a reasonable estimate of the proportion of breeding adults, non-breeding adults, and immatures in the overall population. There was a redistribution of eagles between June and July. Nevertheless, the proportion of eagles in the regional population in May and June was very similar to the proportions seen in July and August (Table 3), providing support for the reliability of the data. Furthermore, we found the eagle population on Besnard Lake in July and August was representative of the overall population for the region, showing that the various age classes are more evenly distributed within the study area at this time (Gerrard et al. 1990).

The percent of adults not associated with nests on Besnard Lake (27–40%) shows that a significant proportion of the adults do not breed. Observations of marked birds suggest that the majority of these are the younger adults (4 and 5 years of age) and these were more numerous in our study than on Amchitka Island where essentially none were observed (Sherrod et al. 1976), and less numerous than the 86% of adults found not breeding in 1979 in southeast Alaska (Hansen and Hodges 1985). A low rate of non-breeding eagles on Amchitka Island may

have reflected the changing status of that population, which appeared to be increasing during the study period, perhaps as a result of the increased availability of food in winter. Evidence from elsewhere is also consistent with the concept that where food resources are not limiting, Bald Eagles will breed at four years of age (Nye 1983). Hansen and Hodges could not explain the high rate of non-breeders in southeast Alaska, although a decrease in food resources was mentioned as a possibility. Our finding that eagles in northern Saskatchewan may not begin breeding until age six suggests that in this saturated population, eagles may have to delay breeding until they are able to compete successfully for the limited breeding territories and the associated fish resources.

Our estimates for adult mortality suggest that it is likely between 6.5% (seen with maximum decline in mortality over the first six years) and 7.7% (estimated with mortality unchanged after the first year).

ACKNOWLEDGMENTS

The authors acknowledge the help and inspiration of Douglas W.A. Whitfield in the earlier years of the Besnard Lake Studies. We thank A.R. Harmata, C.S. Houston and R.W. Nero for helpful comments on the manuscript, and B. Doan for editorial assistance.

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THE *DHO-GAZA* WITH GREAT HORNED OWL LURE: AN ANALYSIS OF ITS EFFECTIVENESS IN CAPTURING RAPTORS

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ABSTRACT.—Trap effectiveness and potential factors affecting success of the *dho-gaza* with Great Horned Owl (*Bubo virginianus*) when used as a lure were examined for 11 species of diurnal raptors and 3 species of owls: Black-shouldered Kite (*Elanus caeruleus*), Northern Harrier (*Circus cyaneus*), Cooper's Hawk (*Accipiter cooperii*), Northern Goshawk (*A. gentilis*), Red-tailed Hawk (*Buteo jamaicensis*), Red-shouldered Hawk (*B. lineatus*), Swainson's Hawk (*B. swainsoni*), Ferruginous Hawk (*B. regalis*), Prairie Falcon (*Falco mexicanus*), Merlin (*F. columbarius*), American Kestrel (*F. sparverius*), Spotted Owl (*Strix occidentalis*), Great Gray Owl (*S. nebulosa*), and Great Horned Owl. The technique was successful for most species when targeting a territorial pair during the reproductive cycle. Important conditions necessary for good trapping success were placement of the lure owl in an obvious location, shade for lure owl and net, shrubs or trees in which to hide net poles and channel the raptors, short distance between observer and net, site preparation, small number of observers, and low wind. Play-back of audio-taped recordings of Great Horned Owls or conspecifics usually reduced the amount of time necessary to facilitate capture. Swainson's Hawks and Ferruginous Hawks showed no increased aggression toward the lure owl that might be related to age of young, brood size, presence of food in the nest, or time of day.

La *Dho-gaza* con Búho Cornado Americano como señuelo: un análisis de su efectividad en la captura de aves rapaces

EXTRACTO.—La efectividad de la trampa y los factores potenciales que afectan el éxito de la *Dho-gaza*, cuando rapaces de la especie *Bubo virginianaus* fueron usadas como señuelo, han sido examinados para 11 especies de raptores diurnas y 3 especies de búhos: *Elanus caeruleus, Circus cyaneus, Accipiter cooperii, A. gentilis, Buteo jamaicensis, B. lineatus, B. swainsoni, B. regalis, Falco mexicanus, F. columbarius, F. sparverius, Strix occidentalis, S. nebulosa,* y *Bubo virginianus.* La técnica dio buen resultado para la mayoría de las especies cuando tuvo como blanco una pareja de aves rapaces en su territorio y en su ciclo reproductivo. Importantes condiciones necesarias para una exitosa trampa fueron: la colocación del búho-señuelo en una ubicación obvia, sombra para el búho-señuelo y la red, arbustos o árboles para ocultar los palos de la red y encaminar las raptoras hacia la trampa, cortas distancias entre observador y red, preparación del sitio, pocos observadores, y viento leve. Reproducciones de grabaciones del ulular de los búhos (*B. virginianus*) o de su especie usualmente redujeron el tiempo necesario para facilitar la captura. Las raptoras *B. swainsoni* y los *B. regalis* no demostraron un aumento de agresión hacia el búho-señuelo que pudiera ser relacionada con la edad de los jóvenes, el tamaño de la nidada, la presencia de alimentos en el nido, o lo hora del día.

[Traducción de Eudoxio Paredes-Ruiz]

A variety of traps have been applied to capture raptors (Bloom 1987). Few traps equal the success of a *dho-gaza* with a live Great Horned Owl (*Bubo virginianus*) lure. The technique, first developed by Arab and Persian falconers (Meredith 1943), was first used extensively in North America by Fran Hamerstrom (1963, Bub 1991). The Hamerstroms used the trap with great effectiveness in their study of Northern Harrier (*Circus cyaneus*) ecology in Wisconsin. A minimum of 18 species, including both nocturnal and diurnal raptors, have been caught using this technique (Bloom 1987). While design and general use of the *dho-gaza* with Great Horned Owl have been well described (Meredith 1943, Hamerstrom 1963, Bloom 1987) its success rate and application have not. In this paper we describe the overall success and applicability of the *dho-gaza* when used on 14 species of raptors.

STUDY AREAS AND METHODS

Trapping took place in four of the western United States and one Canadian province. Most studies were unrelated, conducted over multiple years (1981–92), and conducted by the co-authors working independently or in various combinations. As a result, some differences in trap design and application exist. In general they follow a blend of designs and procedures outlined in Hamerstrom (1963) and Bloom (1987). With the exception of Prairie Falcons (*Falco mexicanus*) in Idaho trapped during incubation, most trapping bouts were conducted after hatching, but before dispersal of young.

PHB, EHH, JLH, BW, PJD, JRB, RLA and MDM used a standard 2.1 m × 5.5 m mist net (210 denier, 2 ply, 10.2 cm mesh; Avinet Inc., Dryden, NY), occasionally two nets in V-shape. Mist nets have the advantage of being large placing poles far apart and can be purchased ready-made (Bloom 1987). The mist net was lightly attached to the poles with clothes-pins and smooth tape tabs (Bloom 1987) or a small piece of limp wire (Hamerstrom 1963) so that the net detached as the bird struck it. The degree of "hair triggering" necessary is dictated by wind conditions and size of the raptor. Placing more tape inside the clothes-pin generally requires more mass, or a stronger wind to pull the net down. JKS used whole mist nets, hand tied nets, or nets made from gill netting with a border added. The smaller handmade nets (ca. 1.5 × 3 m) were attached to wooden poles with clips; the larger mist nets remained attached to poles that collapsed fully or partially on capture. For Merlins (*F. columbarius*), KT and PFS used a single five-tiered mist net 2.1 m × 9.1 m (6.1 cm mesh) attached to three poles with rubber shock absorbers to form a "V" shaped net. This modified mist net did not break away or slide (Clark 1981) like a *dho-gaza* so as to avoid repeated net damage and repairs from tanglement in low brushy vegetation. TLM and JOM made a V-shape using two handtied nets 1.2 m by 1.8 m (10.2 cm mesh) for Prairie Falcons.

The lure owl was centered just out of reach of the net, tethered with a swivel and leash to the ground, a 0.3 m tall log or a portable ring perch 0.5 m above the ground. Observers were in a blind <15 m away, concealed under camouflage 5–100 m away or in a vehicle 0.1–>1 km.

Many territories were trapped at repeatedly; hence trapping the same territory for 3 yr equaled three territories. However, multiple trapping attempts at the same territory in the same year were considered as one territory When possible, we evaluated the success of our trapping efforts using two techniques. We defined "territory trapping success" for a species as the total number of individuals captured divided by the total number of possibilities, where possibilities equaled both individuals of a pair at a territory. "Raptor trapping success" was the number of individuals captured, divided by the number of birds that made contact with the net. Raptor trapping success does not reflect instances when a raptor made a pass over or around a net, was vocal but made no pass, or was present, but engaged in other activities such as copulation, incubation, or territorial defense from other avian competitors.

The sex of raptors was determined by wing length, body mass, brood patch evaluation, behavior, relative size compared to their mates, and the literature (Clark and Wheeler 1987).

Trapping of Black-shouldered Kites (*Elanus caeruleus*; EHH, JLH, PHB, MDM, RLA), Cooper's Hawks (*Accipiter cooperi*; PHB, EHH, JLH), Northern Goshawks (*A. gentilis*; PHB, BW, PJD, RLA, EHH, JLH), Northern Harriers (PHB, EHH, JLH), Red-tailed Hawks (*Buteo jamaicensis*; EHH, JLH, PHB), Red-shouldered Hawks (*B. lineatus*; PHB, EHH, JLH, MDM), American Kestrels (*F. sparverius*; JRB), Great Horned Owls (PHB, EHH, JLH), Spotted Owls (*Strix occidentalis*; PHB, PJD) and Great Gray Owls (*S. nebulosa*; PHB) occurred in California. Swainson's Hawks (*B. swainsoni*) were trapped in California (PHB, BW, PJD, RLA, EHH, JLH) and Alberta (JKS). Ferruginous Hawks (*B. regalis*) were trapped in Alberta (JKS). Prairie Falcons were trapped in Idaho (TLM) and Colorado (JOM). Merlins were trapped in central Alaska (KT, PFS).

JKS captured 414 Swainson's Hawks and 146 Ferruginous Hawks during the 12 years between 1975 and 1991. In 1985–86, trapping time and hawk response was recorded on data sheets; these data form the basis for the Alberta Swainson's and Ferruginous Hawk analyses.

Results and Discussion

Black-shouldered Kite. Southern California kites nest in oak woodland and riparian communities and hunt primarily in grasslands. They act aggressively toward any larger raptor during the breeding season. Of 22 kites attempted at 11 territories by EHH, JLH, MDM, RLA and PHB, 15 were captured including four pairs. Territory trapping success was 68% and raptor trapping success was 100%. Eight kites were caught in <15 min, two required 30 min, and no escapes occurred. Two other Black-shouldered Kites aggressively attacked the owl but were aware of the net and avoided it. One male was recaptured 2 months later at a new territory.

Northern Harrier. Northern Harriers nest on the ground in grasslands, marshes, estuarine habitats in low vegetation. When faced with a Great Horned Owl near the nest they attacked promptly, initially avoiding the net for several passes until caught, possibly because in most situations there were no trees or shade to disguise the net.

PHB, EHH and JLH attempted to capture six harriers at three territories and caught five which included two pairs and a female. Territory trapping success was 83% and raptor trapping success was 100%. The male of the pair at the third territory could not be caught, possibly because he had been previously trapped in a *dho-gaza* the year before. In both instances where pairs were caught, the female

was captured first within 30 min of trap placement. Males were caught within 1 hr of the time the net was reset.

Cooper's Hawk. Cooper's Hawks are aggressive accipiters that nest in oak woodlands in southern California. Their smaller size contributes to their speed and agility giving them the ability to dodge some nets or escape when a net gets entangled in understory vegetation. The odds of capture are balanced by their persistent aggressiveness. EHH, JLH and PHB trapped at 31 territories yielding a territory trapping success of 52% (32) and a raptor trapping success of 76%. Twenty-two females and 10 males were captured including 5 pairs; of which the female was caught first in 4 of the pairs. There were ten escapes, eight females and two males. Four other escapes were followed by capture minutes later. One male, after having its mate caught in the first 2 min, escaped twice and made four other passes before being captured in 40 min. One female escaped after 5 min, then 50 min later both male and female hit the two nets simultaneously but escaped. Nine days later the female was captured in 10 min. She had been captured in the same territory in the two preceding years. Two males and five females were captured twice and two females were captured three times over a 4 yr period.

Capture times of eight males averaged 27.3 min (SD = 23.9, range 2–60 min). Three males were captured in <5 min and five required 30–60 min because either they escaped, the female was caught first, or the set was made at a nearby Red-shouldered Hawk nest. Capture times for 13 females averaged 21.5 min (SD = 20.2, range 1–60 min). Four females were captured in <5 min and six were caught in 10–25 min. Three required 45–60 min after escapes or sets made at nearby Red-shouldered Hawk nests. Capture times were not recorded for the remaining 12 hawks. Two pairs were captured in <5 min. In one case, the female hit a net as the male was removed from the other net. He was the only Cooper's Hawk to be captured twice in the same year. Of the five pairs captured, the female was captured first on four territories.

Northern Goshawk. Goshawks are legendary for their aggressive displays when defending their nests (Bent 1937). They nest in dense coniferous forest, so it is not difficult to hide the net and poles or to keep the owl shaded and cool.

BW trapped at 27 territories in northern California (1986–91) yielding a territory trapping suc-

cess of 76% (41); 21 females and 20 males including 15 pairs. Two fledglings were also caught. Raptor trapping success for 51 goshawks was 86% (44). In the majority of instances when only one member was caught, it was due to the absence of the mate. Males were absent on five occasions and females on two occasions. In one instance each, a male or female left the nest area, and in two instances the female, though present, would not attack the owl. The fastest successful trapping attempt involving a pair was 1 min for the female and 2 min for the male. Time to first capture was <1 hr for 19 of 24 attempts and ranged as high as 155 min. Time to the capture of the mate (following reset) was <1 hr for 7 of 11 attempts and went as high as 180 min before quitting the effort. Most male captures occurred within 1 hr of sunrise before they began hunting and left the nest area. The presence of females at the nest was more dependable, particularly when young were less than half grown.

PJD trapped in northern California at 25 territories yielding a territory trapping success of 54% (27); 6 pairs and 15 individual females. No birds were captured in three territories. Nine females had been captured in dho-gazas in previous years. The lower territory trapping success of this effort relative to others reported for this species may be due to the large number (frequently >4) of observers. Raptor trapping success was 96%.

In northeast California, PHB, RLA, EHH, and JLH (1981–91) trapped at 51 territories yielding a territory trapping success of 67% (68); 45 females and 23 males including 17 pairs. One fledgling was also caught. One male from 2 yr earlier and one female from 8 yr earlier were recaptured. Many goshawks were recaptured the same day or within the same week when attempting to capture a mate. Raptor trapping success was not measured, but was estimated at 80–85% of the hawks that hit the net. Reasons for escapes included perching on the net poles causing the net to detach, tearing through the net, striking the top of the net, and becoming disentangled. One particularly tenacious female tore through the net and escaped three times in 2 hr, only to be caught on her fourth attempt. Minimum capture time for a pair at a previously untrapped territory was 10 min, which included net replacement time. Some goshawks required up to 5 hr to capture. Freshly killed nestling and fledgling passerines and piciformes were found in the net with the goshawk on several occasions.

Few comparative studies of trapping success have been described for the many different types of traps available (Bloom 1987). However, the work of Karlbom (1981) and Kenward and Marcstrom (1983) using compartment traps and bow nets provides useful data for comparisons of the effectiveness of different traps. Whereas time to capture goshawks using Great Horned Owls and dho-gazas was measured in minutes or hours, time to capture using compartment and automatic bow-nets has been measured in trap-days (Karlbom 1981, Kenward and Marcstrom 1983).

Red-tailed Hawk. In southern California, Red-tailed Hawks nested in oak and riparian woodland habitats. In contrast to the other three Buteos, Red-tailed Hawks responded poorly to a Great Horned Owl and net near their nest site. EHH, JLH, and PHB trapped at eight territories (in 1986 and 1992) yielding a territory trapping success of 13% (2) and a raptor trapping success of 100%. Both hawks, a male and female, required ≤5 min.

In northern California Red-tailed Hawks nested in juniper-sage habitat. BW trapped at nine territories (1990) yielding a territory trapping success of 17% (3) and a raptor trapping success of 100%. Time to capture for the two females and one male was 10–60 min. One other Red-tailed Hawk made an aggressive stoop at the owl, missed the net, and ceased attacking.

Red-shouldered Hawk. Red-shouldered Hawks in southern California nest in oak and riparian woodlands. Most hunting is from perched positions under the forest canopy where long distance visibility is limited (McCrary 1981, Bloom 1989). As a result Red-shouldered Hawks usually do not locate the owl immediately in the same way a Swainson's or Ferruginous hawk could from their aerial positions.

PHB, EHH, JLH and MDM trapped at 132 Red-shouldered Hawk territories (1979–91) yielding a territory trapping success of 75% (199); 102 females and 97 males including 53 pairs. Raptor trapping success for 87 attempts was 95% (83). Four escapes included two males and two females. Of 20 pairs, females were caught first on 5 occasions, males on 15.

Capture time for 23 female Red-shouldered Hawks unfamiliar with a dho-gaza averaged 76.1 min (SD = 73.9, range 5–300 min) and 10 males averaged 63.5 min (SD = 53.4, range 5–180 min). Recapture time in the same or different years was considerably longer. Ten females averaged 181.0 min (SD = 138.3,

range 30–525 min) and seven males averaged 124.3 min (SD = 109.5, range 5–290 min).

Swainson's Hawk. Swainson's Hawks are a *Buteo* of open habitats, frequenting deserts and agricultural areas with sparse trees. As a result, camouflaging the net and poles is usually difficult and sometimes impossible. Even with a net erected with no trees to hide it, many Swainson's Hawks stooped on the owl, sometimes from several hundred meters high or from a nearby perched position. Good sets allow placement of one or both poles next to or between two trees, particularly if shaded. The drawbacks of trapping in arid situations are heat on the lure owl during midday, and the winds that frequently occur in desert areas in the late afternoon. Winds cause the net to detach or billow and become more obvious. Because some territories were composed primarily of rock fields, we sometimes had to place the trap 150 m from the nest tree to find a safe landing area for the hawk.

Most Swainson's Hawks are very aggressive toward Great Horned Owls placed within 100 m of the nest. Of 132 Swainson's Hawks attempted by BW (1985–91) 98 were captured yielding a raptor trapping success of 74%; 44 females and 52 males including 32 pairs. Of 32 pairs, females were captured first 19 times and males 13 times. At two territories both polyandrous males were caught first. On six occasions no hawks were captured because of wind and absence of hawks. Hawks with territories in poor quality habitat (Woodbridge 1991) seemed less tenacious and less likely to be present to defend the territory.

In northeast California (1981–88) PHB, EHH and JLH trapped at 58 territories yielding a territory trapping success of 63% (73); 30 females and 43 males including 17 pairs. Of 17 pairs, females were first into the net on 8 occasions and males on 9 occasions. Raptor trapping success was not quantified but was estimated at 75–85%. Escapes from nets occurred most frequently in the first years of trapping when we used vehicles as blinds and parked 0.25–1.0 km from the net. The few minutes travel time to the net allowed >10 individuals to escape. Escapes were reduced in later years by using a blind.

In the Central Valley of California (1985–91) RLA and PJD trapped at 54 Swainson's Hawk territories yielding a territory trapping success of 62% (67); 33 females and 34 males including 17 pairs. At least one member of a pair was captured in 50 of 54 territories. Of the 17 pairs captured,

females were caught first on 13 occasions and males on 4. Raptor trapping success was not measured but was estimated at 80–90%. Thirteen Swainson's Hawks previously trapped in *dho-gazas* were later recaptured for transmitter replacement or removal.

Of 194 trapping attempts over two years at 192 Swainson's Hawk territories in Alberta, JKS captured 34% (129) of a possible 384 hawks. This low territory trapping success of 34% may be because in this study an attempt was made to capture a large number of hawks. Trapping in any one territory was rarely repeated within one year. During the first 30 trapping attempts in 1985, raptor trapping success was 68%.

When time from leaving the setup to capture was considered, females were captured sooner than males in Alberta. When considering a particular sex that was caught alone or caught first in the case of a pair, 46 females were caught on average in 7.2 min (SD = 5.8, range 0–45 min) and 63 males in 13.2 min (SD 12.8, range 0–45 min). The later capture of males was not significantly different (χ^2 = 5.94, df = 2, P = 0.051) and may have been due to some males arriving at the nest after the *dho-gaza* had been set up. Combining data from all trapping of Swainson's Hawks revealed that for a total of 86 pairs captured, females were caught first on 46 occasions (53%) and males first on 40 occasions (47%).

Ferruginous Hawk. A tree and cliff nesting raptor of open country, desert and grasslands, the Ferruginous Hawk was more timid than the Swainson's Hawk when defending the nest against a Great Horned Owl as a lure. In Alberta, JKS trapped at 177 territories a total of 191 times yielding a territory trapping success of 19% (66); 27 females and 39 males including five pairs. Of all pairs females were caught first. Raptor trapping success for the first 30 Ferruginous Hawks captured in 1985 was 68%. Distance between a well hidden observer and net should be small since Ferruginous Hawks frequently broke free from the net. After trap setup and departure, females took on average 17.0 min to be caught (SD = 14.1, range 3–55 min); males averaged 16.2 min (SD = 16.2, range 0–62 min).

Prairie Falcon. Accounts of the ferocity with which Prairie Falcons attack owls during the nesting season are well known and mortal strikes are not uncommon (Bent 1937). Fortunately, because the lure owl does not fly, the risk of physical contact from the falcon is minimal. Another concern is for the safety of the falcon; since rocks are commonly

found near the cliff trapping location. The area where the falcon will likely land after entanglement should be free of rocks.

Owing to the focus of the study (radio telemetry), TLM attempted to trap only one member from each pair in the Idaho Great Basin Desert, resulting in 16 females and 6 males captured (Marzluff et al. 1991). Average length of time needed to capture a falcon was 40 min for 26 attempts and ranged from 5–180 min. In the Colorado Pawnee Grasslands (1976–78) where the objective was to capture both members of each pair, Steven W. Platt and JOM caught 14 pairs, 34 individual female and 18 male Prairie Falcons (Platt 1981). Of 47 attempts to re-capture marked falcons, 5 (11%) were successful. Less than 10% of the falcons escaped after striking the net in either study, yielding a raptor trapping success of approximately 90%.

Merlin. Merlins were trapped on open tundra, white spruce taiga and riparian willow shrub communities in central Alaska. KT and PFS (1987–89) trapped at 43 nest territories yielding a territory trapping success of 90% (77). Eight males and one female were not captured. Two males were not present during trapping so no chance existed for their capture. The uncaptured female had been caught in a previous year. Five females and six males previously trapped with a *dho-gaza* were recaptured. Raptor trapping success was 100%.

In the typical situation the female was captured within a few minutes and usually held until the male was caught to avoid her recapture. Males were often initially absent. If the female was present, the male arriving with prey presented it to her and left before discovering the owl. In the absence of the female the male would remain in the nest vicinity, possibly cache the prey item, and attack the owl as soon as it was discovered. Freshly killed passerines were often recovered from the net or picked up nearby.

Even on windy days the antagonism Merlins demonstrated toward Great Horned Owls overcame their reluctance to fly into the nets. Merlins frequently struck the nets, bounced out, and were caught on the next pass.

American Kestrel. In this study American Kestrels nested in oaks, and sycamores surrounded by grasslands. They responded quickly to an owl in their breeding territory and usually were caught if they struck the net. In fact several of us inadvertently caught kestrels when attempting to capture other species. JRB attempted 118 kestrels (1983–90) and

captured 115 for a raptor trapping success of 97%. Six other kestrels aggressively stooped on the lure owl but did not make contact with the net. Because kestrels lacked the mass necessary to easily dislodge corner tabs of a mist net, the tabs must be "hair triggered" to detach easily. Using smooth tape and weakened clothes-pin springs was important. This causes some problems on windy days but greatly increased trapping success.

Spotted Owl. Spotted Owls show a strong affinity toward mature coniferous forests where shade is an inherent part of the territory. Site preparation involves removal of branches in adjacent trees and the area on the ground where the owl would come to rest after striking the net. Placement of the net was normally accomplished with adults nearby.

PJD and PHB made eight diurnal attempts at four territories that yielded three pairs with none captured at the remaining territory. Territory trapping success was 75% (6) and raptor trapping success was 100%. When there was no response from either adult Spotted Owl after 30–60 min, a "branching age" Spotted Owl chick (one of their young) was held near the Great Horned Owl in front of the net and in six attempts six owls were caught. However, one adult owl was caught without a young owl in hand the day after its mate was caught. While young of branching age were present in the trees at the fourth Spotted Owl territory, only the female responded, with four passes over the net. Even though the lure owl was less than 50 m from the branching owlets, the lack of an immediate threat (relative to the above three instances) to its young and the more advanced age of these young relative to those in the above territories may have diminished the defense response.

Great Gray Owl. In California Great Gray Owls nest in tall snags in upper elevation coniferous forests and meadows of the Sierra Nevada Mountains. PHB made single diurnal net sets at three Great Gray Owl nests. Adult female Great Gray Owls were captured on all three occasions in <3 min. Territory trapping success was 50% and raptor trapping success was 100%. Although present on two occasions, no male Great Gray Owls attempted to strike the lure owl. Great Gray Owls responded very aggressively, sometimes with the intent of binding to the lure owl, even with the observer <5 m away.

Great Horned Owl. In coastal southern California Great Horned Owls most frequently nest in oak and riparian woodlands, using abandoned nests or

sandstone potholes. Of 16 attempts at 8 Great Horned Owl territories PHB, EHH and JLH captured 4 females and 1 male. Territory trapping success was 31% (5) and raptor trapping success was 56%. Four other owls escaped after brief entanglement. All captures and escapes were <15 min after setup, except for one male which escaped 75 min after its mate escaped. All attempts were made at dusk except for one early morning capture of the male.

Several setups were removed after the initial attempt owing to the difficulty of extricating an owl from a tangled net and replacing nets after dark. The lure owl was vulnerable to attacks by wild owls which at times attempted to bind to it. The researcher's visibility is also reduced in the darkness.

Raptor Response in Relation to Age of Young. Both sexes of Swainson's and Ferruginous hawks in Alberta exhibited slightly decreased but statistically non-significant declines in capture success as their young grew older (Fig. 1; for Swainson's Hawk females $\chi^2 = 4.30$, df $= 2$, $P = 0.116$, for males $\chi^2 = 0.74$, df $= 2$, $P = 0.691$; for Ferruginous Hawk females $\chi^2 = 0.06$, df $= 2$, $P = 0.972$, for males $\chi^2 = 1.66$, df $= 2$, $P = 0.437$). Aggression by adults seemed strongest when small to half grown young were in the nests. When young were beginning to fledge ("branchers"), fewer adults responded. This was also noticeable with other species, especially goshawks.

Raptor Response in Relation to Brood Size. A body of theory suggests that a parent's investment in reproduction (including nest defense) may be affected by a balance between past versus future expectations of reproductive fitness (e.g., Trivers 1972). There was no evidence that the Swainson's ($\chi^2 = 0.13$, df $= 2$, $P = 0.935$) or Ferruginous hawks ($\chi^2 = 0.40$, df $= 2$, $P = 0.821$) studied in Alberta in-
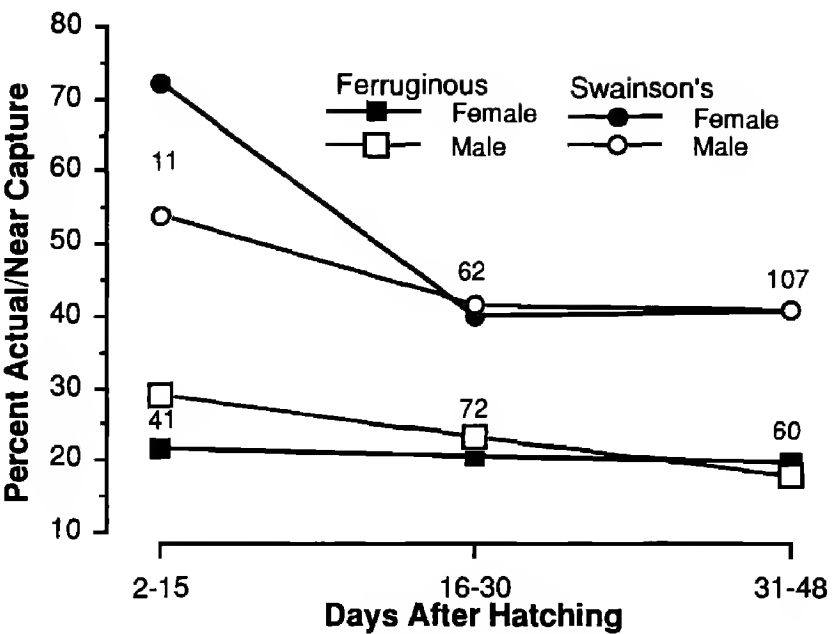

Figure 1. Percent of Ferruginous and Swainson's hawks in Alberta that exhibited strong aggression toward a Great Horned Owl, in relation to age of nestlings. Percent actual/near capture refers to hawks that were either aggressive enough to be caught or aggressive but aware of the net which they maneuvered to avoid. Numbers represent the total number of pairs of each species in each time period.

creased the intensity of defense based on past investment as reflected in brood size (Table 1). It is conceivable that Great Horned Owls represent less danger to young of large buteos as the young approach adult size.

Raptor Response in Relation to Food in the Nest. Hawks may defend their nest more strongly when food is present (Pascual and Santiago 1991). JKS found that protection of food in addition to young probably was not a contributing factor. Of 60 attempts to capture Swainson's Hawks while prey were present in the nest, 29 hawks (48.3%) were caught. Of 124 attempts while prey were absent, 78

Table 1. Success in capturing one or both members of a pair of Ferruginous or Swainson's hawks in relation to the number of young fledged. Percentages are in parentheses.

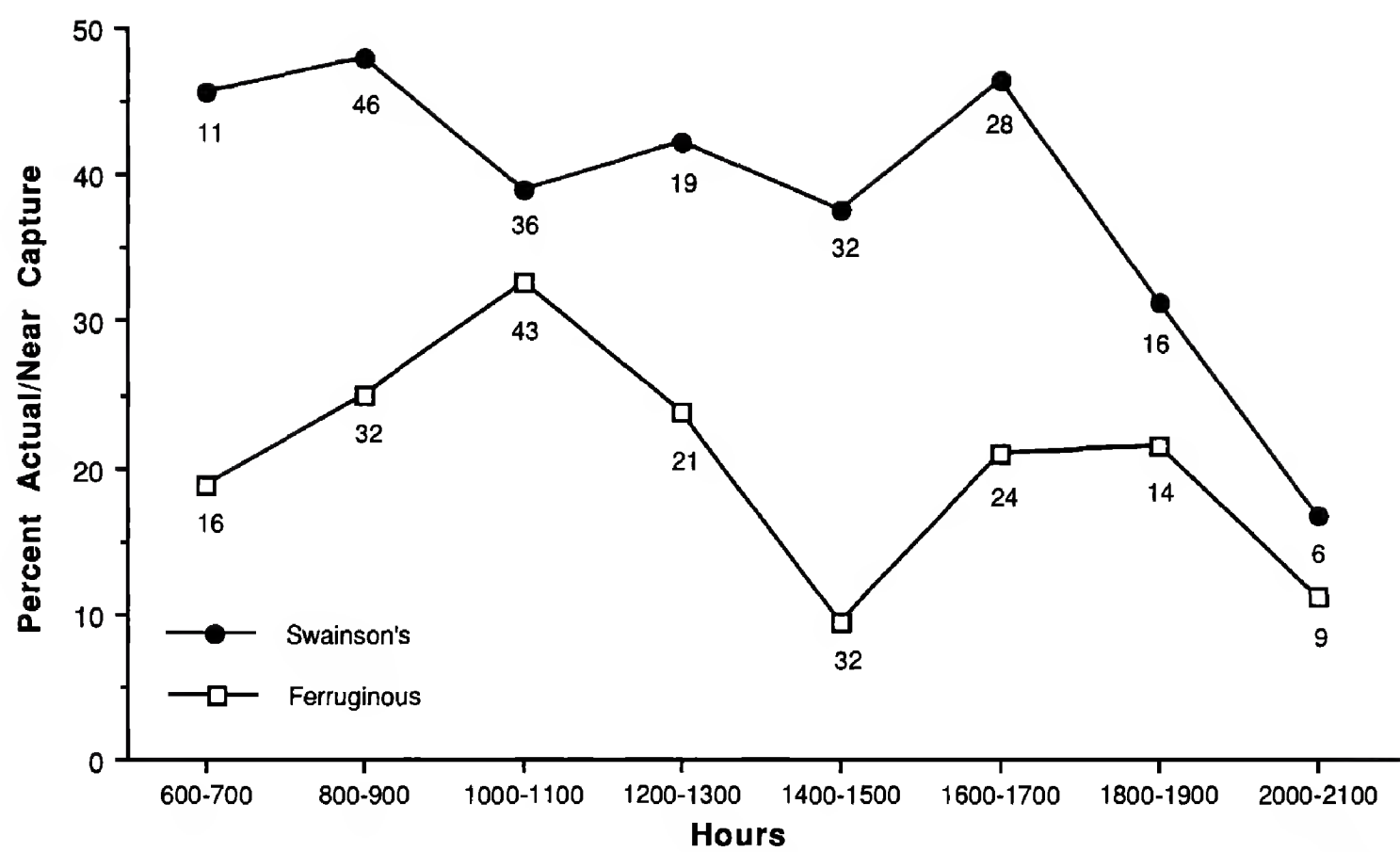| ONE OR MORE ADULTS	NUMBER OF FLEDGLINGS				
	1	2	3	4	5
Ferruginous					
Caught	4 (6.7)	11 (18.3)	20 (33.3)	21 (35.0)	4 (6.7)
Not caught	8 (6.6)	21 (17.4)	46 (38.0)	42 (34.7)	4 (3.3)
Swainson's					
Caught	22 (20.4)	52 (48.1)	31 (28.7)	3 (2.8)	
Not caught	18 (22.5)	37 (46.3)	25 (31.3)	0	

Figure 2.   The proportion of Ferruginous and Swainson's hawks in Alberta that were sufficiently aggressive to be either caught or only narrowly avoid capture in relation to time of day. Numbers below data points represent the number of trapping attempts in this time period.

(62.9%) were caught (χ^2 = 3.53, P = 0.060). Likewise, Ferruginous Hawks did not respond more aggressively to the lure owl when food was in the nest with young. Of 78 attempts to capture Ferruginous Hawks while food was present in nests with young, 21 (26.9%) were successful; of 98 attempts when food was absent 34 (34.7%) resulted in capture of one or more adults (χ^2 = 1.22, P = 0.270).

Aggression in Relation to Time of Day. In Alberta, most of the trapping took place between 0600–2000 H. Within this time span, Ferruginous Hawks exhibited a bimodal pattern of aggressiveness (Fig. 2). The reduced aggression early and late in the day was surprising since Ferruginous Hawks were crepuscular, at least those nesting west of the Rocky Mountains (Smith and Murphy 1973). Swainson's Hawks seemed to exhibit reduced aggressiveness late but not early in the day (Fig. 2).

Care of the Lure Owl. The lure owl is the most critical component of the trap and should be treated as though priceless. A wood stump or log for the owl to stand on or hide behind affords the owl some protection from unusually fierce attacks. Jesses and tether (1 m) should be long enough for the owl to comfortably move about or defend itself should a hawk or owl attempt to bind to the lure owl. Trap-

ping in hot weather should be done only in the early morning or late afternoon and preferably in the shade. The owl can be cooled by regularly misting with water from a spray bottle, and rehydrated by squirting a minimum 40 cc/day (avoid trachea; M.J. Gibson pers. comm.) of Gatorade from a syringe into its mouth. It is preferable to have the owl in sight of the observer to monitor its behavior to determine stress from weather, or the presence of predators including the target raptor.

Of the raptors we attempted to trap, the most serious threat to the lure owl was from the Northern Goshawk, Red-shouldered Hawk, Great Horned Owl and Great Gray Owl. We sustained one injury and four lure owl mortalities. The injury was due to a puncture wound to the head from a Northern Goshawk. Mortalities were incurred from a Bobcat (*Felis rufus*) attack despite the presence of a blind 15 m away, a blow from a Red-shouldered Hawk, and dehydration (N = 2). On several occasions Northern Goshawks and Great Horned Owls have bound talon to talon to our lure owl without any apparent injury to either bird. A nearby blind greatly reduced arrival time of the observer and the chance of an injury to the owl. Nearly 1400 kites, hawks, falcons, and owls in these studies were captured with
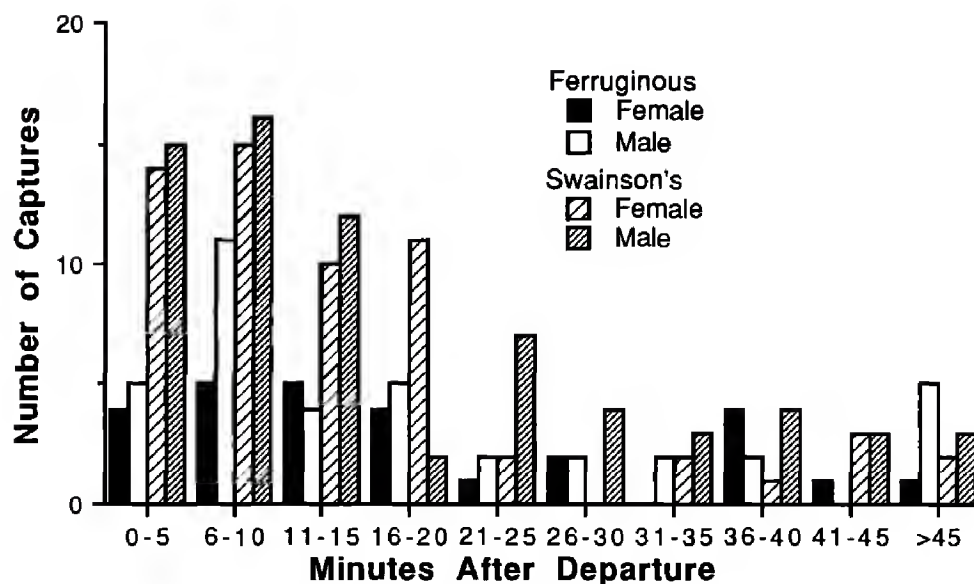
Figure 3.   The number of captures of Ferruginous and Swainson's hawks in Alberta in relation to the time after the *dho-gaza* was left at a nest.

the *dho-gaza* without injury to the target raptor. Although a few lure owl mortalities may be unavoidable, with care the *dho-gaza* with lure owl is a reasonably humane and very effective live trapping device.

Using Raptor Lures Other Than Great Horned Owls. Raptors that have been captured before, escaped, or had unrewarding experiences with traps may become "trap-trained" (Bloom 1987). Even when trap-trained to a lure owl, certain individuals may still attack if the lure bird is replaced with a new species. When trapping Red-shouldered Hawks PHB, EHH, JLH, and MDM used an adult Red-tailed Hawk (McCrary 1989) in 15 territories to capture three female and four male Red-shouldered Hawks that previously could not be recaptured with a Great Horned Owl. Similarly, a Red-shouldered Hawk was used in five Red-shouldered Hawk territories that resulted in the recapture of three trap-trained hawks that would no longer respond to a lure owl. No injuries or mortalities occurred to the lure hawk.

Trapping During Winter. PHB attempted to capture two Black-shouldered Kites, two Northern Harriers, three Red-tailed Hawks, one Ferruginous Hawk, and two Prairie Falcons during winter with no success. The two kites, two harriers, and one Prairie Falcon responded by stooping to within 5 m of the net, but never made contact. Under less open situations with better camouflage the *dho-gaza* may have worked. One Sharp-shinned Hawk (*A. striatus*) was trapped by EHH and JLH on its wintering grounds in southern California, and BW captured

one Rough-legged Hawk (*B. lagopus*) in northern California.

Improving Raptor Trapping Success. It is important to minimize the time spent at a nest. Some species and individuals are more tolerant than others. Some raptors are more vulnerable to disturbance at certain periods in the breeding cycle, particularly incubation. The researcher's experience and ability to assess the effects of weather, time of day, presence or absence of the target raptor, and behavior of the individual during the various stages of the reproductive cycle will determine the amount of time spent at the nest. This may ultimately determine the success or failure of both the trapping and nesting attempt. Of 300 trapping attempts on several species of raptors in southern California, 5 resulted in failures (*A. cooperi, B. lineatus*) during incubation. We suspect that these could be attributed to our disturbance.

JKS's experience in Alberta with Swainson's and Ferruginous hawks was that if capture was not accomplished quickly the likelihood of success decreased substantially (Fig. 3). This decline in aggression could be due to the hawks' aggression being simply of short duration, due to the hawks detecting the unusual way in which the owl (lure) invaded their territory, or both. In some rare cases hawks were captured after 1 hr, but if the object was to capture as many hawks as possible and not necessarily specific individuals, it proved more efficient to go to another territory after 30 min rather than wait for a response. This may not be the case when targeting specific individuals or woodland raptors that may take longer to see the owl.
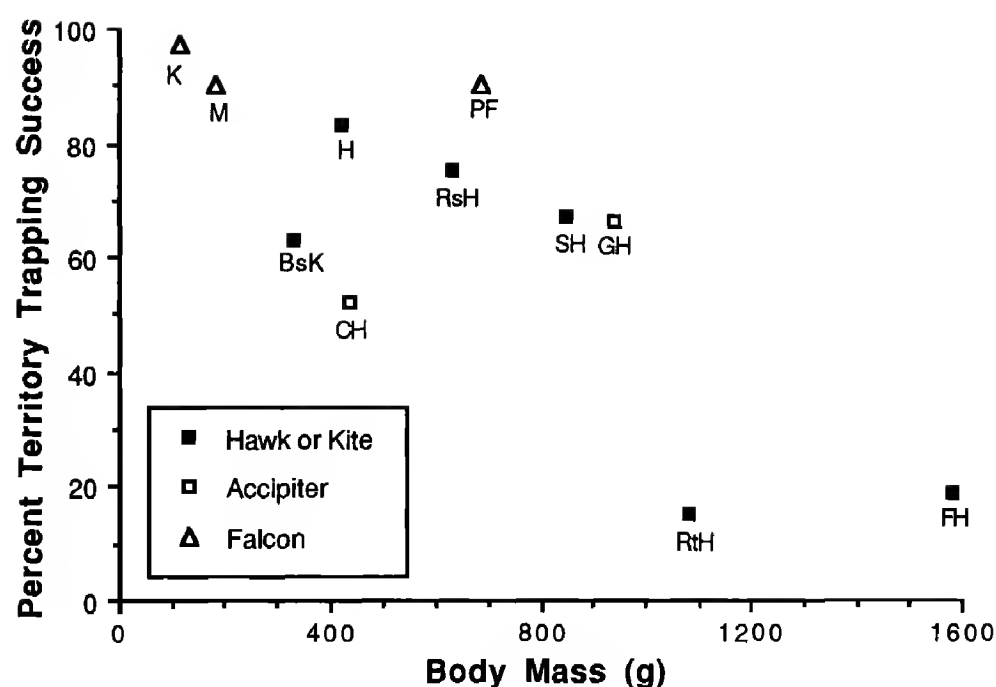
Figure 4. Territory trapping success of the species studied in relation to body size.

While we did not attempt to quantify the effects of human disturbance at trap sites, several of us feel that trapping success and/or time necessary to capture hawks can be affected by the number of participants. Only 1–3 people should attend a trap site. This is particularly true of forest dwelling raptors, which, while present and vocal on arrival of a small group, may disappear if the assemblage increases (Speiser and Bosakowski 1991).

Site selection is critical to trapping success. The owl should be placed in the most visible location possible which also allows for good placement of the net in terms of camouflage, shade and directing the raptor into the net. Proper placement greatly decreases the time to capture. As a rule, the closer the trap is to the nest the stronger the response from the hawk. When possible, nets should be placed between two trees so that the net poles become less apparent and the attacking raptor is forced to fly into the net and not parallel. Shade is equally important, both in terms of keeping the lure owl cool, and hiding the net which is very visible in full sunlight.

Observer position and site preparation are important for capturing individuals who are only loosely caught. The best situation is a portable blind (e.g., Leonard Rue Enterprises, Inc., Blairstown, NJ) placed within 25 m of the net. In the case of breakaway nets, the area in which the raptor is going to fall should be cleared of all large branches, rocks, shrubs and pine cones. This is necessary for the raptor's safety, to ensure a catch and to facilitate removal of the raptor from the net. If the second member of a pair is to be captured, a replacement net can be set and the first bird can be disentangled at another location.

If a breeze is blowing the net should be placed perpendicular to the wind since most raptors attack into the wind. The net can become entangled on the pole and clothes-pins if placed parallel to the wind direction.

Tape recorded vocalizations of either a Great Horned Owl or the target species can decrease the time needed to attract a raptor, particularly woodland species which may not be aware of the lure owl even though only 100 m away. It was noted that some individual goshawks, particularly males, seem intimidated by the call and may leave the area. Once a lure owl has been habituated to the set and refuses to move, a monofilament line attached to its jess can be lightly tugged to create the added stimulus that will cause the raptor to attack.

There was a strong trend for the larger raptors to be more difficult to capture than smaller ones (Fig. 4). Larger raptors also broke free from the net more often which reduced raptor trapping success. Several possible reasons could be advanced for this lowered success with increasing raptor size; among them is the possibility that the nestlings of large raptors may pose a danger for a Great Horned Owl, especially when the nestlings are more than half grown. The primary limiting factor in capturing Swainson's and Ferruginous hawks in Alberta was a lack of response by the hawks toward the owl (Fig. 5). Both members of a pair were almost always present, only a few
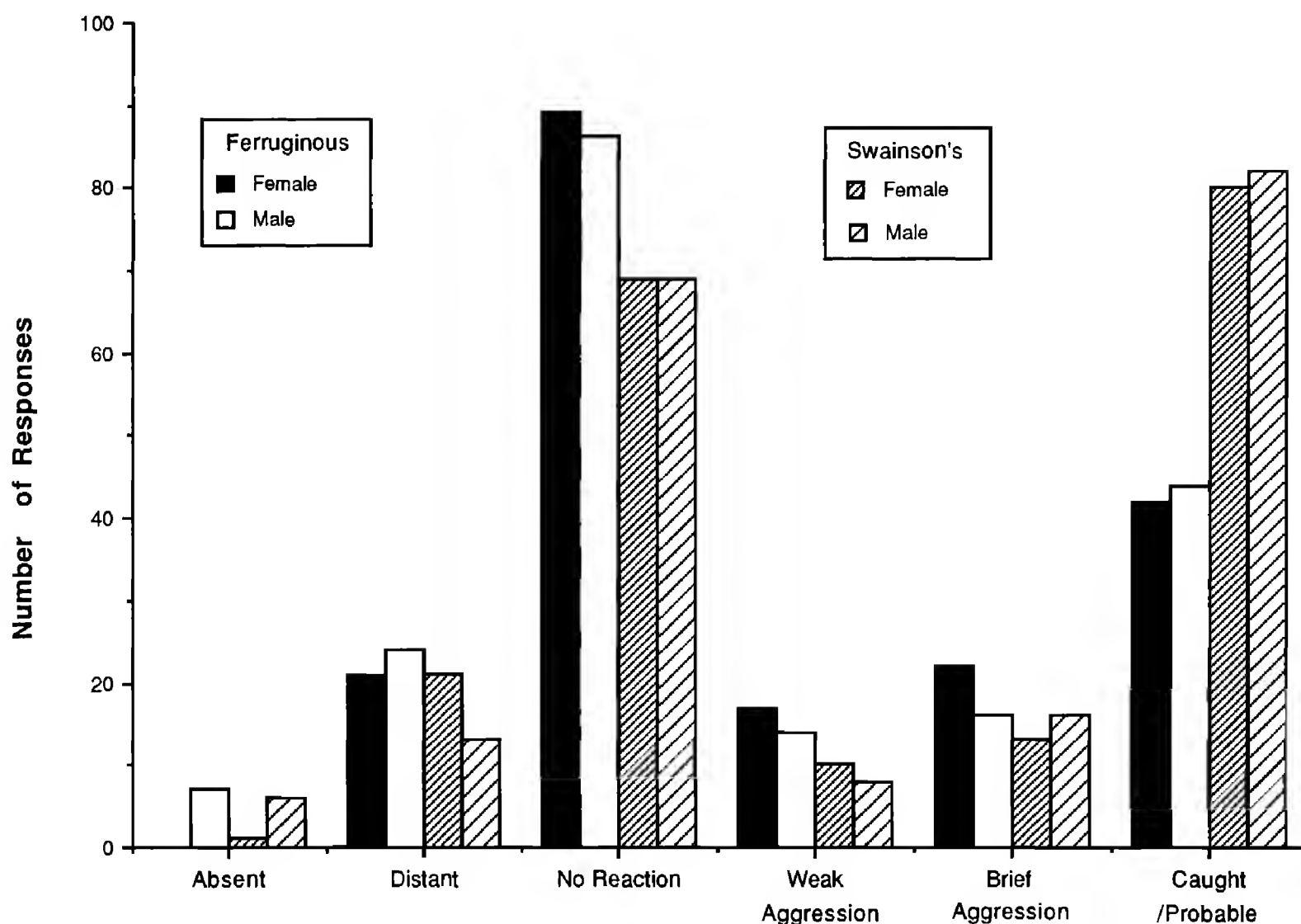
Figure 5. Types of responses by Ferruginous and Swainson's hawks studied in Alberta. Some hawks, usually males, never appeared near the nest, some remained distant (>300 m from the *dho-gaza*) and others exhibited reactions of varying degree. The "caught/probable" category includes those that presumably saw and avoided the net.

remained at a distance unwilling to approach the nest site, but the majority simply failed to respond aggressively.

Another explanation for lowered trapping success and attacks from larger raptor species on the lure owl could be that the more vigorous attacks from smaller raptor species would seem predictable since these species likely have taken the brunt of predation by large *Bubo*s over evolutionary time relative to larger raptor species. Further evidence for this theory is available in the form of the lack of instances of Golden Eagles (*Aquila chrysaetos*) observed stooping at the lure owl during this study, even though Golden Eagles nested on our study areas and attacks by other non-target raptors on lure owls were not uncommon. However, the distance between the *dho-gaza* and Golden Eagle nest sites may have been too great to elicit an attack. None attacked the lure owl suggesting that for Golden Eagles, the largest of buteonine raptors in North America, the Great Horned Owl may only pose a modest threat.

In conclusion, very few traps yield the success of the *dho-gaza* and Great Horned Owl when used in the spring at a raptor's nesting territory (Bloom 1987). Many researchers have used this technique as the number of co-authors, wide region of use, and number of species in this article will attest. Trapping success for a given species may depend upon the individual's aggressiveness and probably a great deal on the individual trapper's experience, techniques and patience. The early development and publication of the use of the *dho-gaza* by Fran and Frederick Hamerstrom (Hamerstrom 1963) has led to use of this technique across North America on a wide variety of raptors and has facilitated research and conservation of birds of prey in important ways. We salute them for bringing this technique back from the many centuries it lay essentially dormant in the Old World.

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CONSERVATION BIOLOGY AND THE EVOLUTION OF A LAND ETHIC

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ABSTRACT.—"Conservation biology" is reportedly distinct from other natural sciences because of its focus on a wide array of biota, the long-term scale at which it operates, its holistic nature, its assumption that organisms have an intrinsic value and its direct application of research to a management goal. However, most of what contemporary conservation biologists endorse was previously proposed by Aldo Leopold, and practiced by two of his former students, Frederick and Frances Hamerstrom. That their work with Northern Harriers (*Circus cyaneus hudsonius*) and Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) has received widespread recognition is a testimony to the effectiveness of this approach. Conservation biology is only now gaining widespread acceptance probably because of the increasing importance that society has recently placed on the environment. Leopold predicted that society's perception of the environment would move towards what he termed a "land ethic" before the approach endorsed by contemporary conservation biologists could be successful. We may be witnessing the stirring of just such a movement.

Biología de la conservación de la naturaleza como un paso en la evolución hacia una "Ética en el uso de la tierra"

EXTRACTO.—La biología de la conservación de la naturaleza es referida como distinta de las otras ciencias naturales; esto es así debido a su enfoque de una amplia gama de la biota, la escala en la que opera, su naturaleza todista y compleja, su asunción de que los organismos tienen un valor intrínseco, y la aplicación directa de sus investigaciones a los objetivos conservacionistas. Sin embargo, la mayor parte de lo que los biólogos conservacionistas contemperáneos rubrican fue previamente propuesta por Aldo Leopold, y practicado por dos de sus discípulos Frederick y Frances Hamerstrom. El trabajo de ellos, con aves de las especies *Circus cyaneus hudsonius, Tympanuchus cupido pinnatus,* ha recibido amplio reconocimiento, lo que es un testimonio de la efectividad de este método. La biología conservacionista, solo recientemente, está ganando amplia aceptación probablemente debido a la creciente importancia que recientemente la sociedad está dando al medio ambiente. Leopold ha pronosticado que la percepción ambiental de la sociedad ha de encaminarse a lo que él llama "Ética en al uso de la tierra," antes de que el método seguido por biólogos conservacionistas pueda tener resultados con éxito. Quizás estemos testimoniando la animación de tal movimiento.

[Traducción de Eudoxio Paredes-Ruiz]

The term "conservation biology" describes a new and developing field with a unique focus and approach to addressing conservation problems (Soulé 1985). The emergence of the Society for Conservation Biology in 1985 (Soulé 1987) and the rapidity of its acceptance in the biological sciences clearly suggest a real need for the group. A review of the early literature reveals that conservation biology as an approach to biological problems emerged almost 50 years earlier when Paul Errington and Frederick Hamerstrom (1937) described their profession of wildlife management as "the new and growing field of conservation biology." Subsequently, in a chapter in his Sand County Almanac entitled "The Land Ethic," Leopold (1949) discussed the philosophical justification for this approach and predicted its staged development. Here, I develop the argument that contemporary conservation biologists follow the approach of Leopold and his former students, Frederick and Frances Hamerstrom. I provide support for this notion by examining Leopold's "Land Ethic" for the underlying theme of conservation biology, and by tracking his ideas through case studies including the Hamerstroms' work on Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) and Northern Harriers (*Circus cyaneus hudsonius*). I also address the question as to why conservation biology is only now gaining widespread acceptance, and discuss the pivotal role of society's perception of conservation.

CHARACTERISTICS OF CONTEMPORARY CONSERVATION BIOLOGY

Contemporary conservation biology is said to be on the interface of science and policy, and as such is frequently referred to as a crisis or mission-ori-

ented discipline that incorporates both science and art (Soule 1985). The primary goal of the discipline is to preserve global biological diversity (Soule 1985, Gavin 1986, Murphy 1990).

Soule (1985) included the following characteristics in his definition of conservation biology: 1) its belief that biological resources have some inherent value beyond that of economic gain, 2) its focus on a wide array of biota, 3) the scale in which it operates (e.g., goals are often stated in terms of long-term viability rather than short-term production and maximization), 4) its holistic approach both to the level of study (i.e., it focuses on communities, systems and processes as well as species) and to the participating disciplines (i.e., it relies on social sciences, economics, philosophy, earth sciences and biology), 5) the direct application of its research toward management (Murphy 1990).

THE LAND ETHIC AS A FRAMEWORK FOR CONTEMPORARY CONSERVATION BIOLOGY

Leopold (1949) described conservation as the ability to understand and preserve the capacity of the land for self-renewal, and as "a state of harmony between men and the land." Leopold used the term "land" to represent all things, biotic and abiotic, associated with the earth. He realized that humans must exist as an integral component of the land rather than apart from it as a separate entity. Indeed, changing people's perception from one of "conqueror" of the land to that of "member" is the essence of the "Land Ethic."

Contemporary conservation biologists warn against an anthropocentric view wherein the value of a biotic community is determined solely on economic grounds (Soule 1985, Callicott 1986, 1990, Norton 1988, but see Kellert 1986), and where conservation efforts would therefore be necessarily restricted to relatively few species. This contrasts sharply with that of most conservationists during the early 1900s when natural resources were viewed as commodities to be consumed by all (Callicott 1990). Indeed, it was under these prevailing conditions that Leopold was trained as a forester and subsequently employed by the U.S. Forest Service (Meine 1988) to implement production-oriented management practices. Leopold crystallized many of his ideas in his book "Game Management" (Leopold 1933). Although the title suggests an exclusive orientation toward economically important species, Leopold (1933) suggested that the objective of both game and nongame management

should be to allow people the opportunity to admire and enjoy all types of wildlife. Leopold (1949) further articulated his belief that a biotic community composed solely of economically important species could not function properly. He stated that economically unimportant species "are members of the biotic community, and if (as I believe) its stability depends on its integrity, they are entitled to continuance." He explicitly reminded us that all members of the biotic community are valuable because it is their membership that defines and perpetuates the functioning system. Each member, therefore, has an intrinsic value not necessarily related to its use to humans. As a closing comment on the subject Leopold (1949) cautioned that economics must play a role in defining the limits of land use, but it is imperative that economics not become the sole determinant of all land use. He suggested this would be the greatest obstacle to the development of a land ethic.

Leopold (1949), like contemporary conservation biologists, shared the belief that to be effective conservation must be multidisciplinary. He recognized that education can provide the basis for an understanding of the land, yet he was not satisfied with what higher education was providing. The idea that ecological knowledge was simply obtained through the study of ecology ran counter to his broad approach to conservation. Specifically, he believed it was proper and necessary for ecologists to be trained in economics, history, geography, botany and agronomy.

Perhaps the strongest link between conservation biology and Leopold's Land Ethic is the holistic theme of interconnectedness, communities and system integrity. Specific references to this theme include the extension of his discussion on the economic importance of species to include that of communities. He also warned that government could not manage for most ecological communities because they occurred on what we now call a landscape scale, often interspersed with private properties. Similarly, contemporary conservation biologists frequently insist that conservation problems do not recognize political boundaries and, therefore, solutions must address the issue of scale.

Leopold further emphasized the importance of communities and systems by presenting the notion of nutrient cycling and food webs as one of the most basic attributes of the land, and energy as the common currency of all systems. He suggests that evolution increases the diversity of the land and implies

that a system's health depends on its ecological diversity. Conversely, Leopold notes that changes in systems occur naturally, but that the disruption of the nutrient cycle caused by mechanized humans is more profound than ordinary evolutionary changes. Like conservation biologists today, he warned that human-induced changes reduce diversity and simplify once complex systems.

OF HARRIERS, MICE AND DDT

In the spring of 1957 the curiosity of Fran Hamerstrom directed her to a question: do harriers mate for life? In the following years this question developed into a series of additional questions, answers, and, most importantly, a framework to address a devastating conservation problem that had not yet reared its ugly head (Hamerstrom 1986).

Because of a paucity of data during the early years of wildlife management, most information was obtained through direct observation. So it was with Hamerstrom's harrier study where answers to the initial question of mate fidelity led to innovative techniques, such as color-marking, molt sequencing, and the determination of age and sex criteria for harriers (Hamerstrom 1986). The realization that harriers do not mate for life led directly to the broader question of what governs their mating system. The subsequent long-term investigation of this question focused on a wide range of factors affecting harrier populations. Information was collected on nest-site fidelity, mate fidelity, courtship behavior, productivity, nestling development, food items, home ranges, population indices, migration patterns, age structure, agriculture practices, and the relationship between harriers and their prey species. The interaction between harriers and their prey was further examined by measuring prey species composition, their annual abundances, reproductive output, sex ratios, age ratios and physical attributes. Collectively this broad body of knowledge led Fran Hamerstrom to two important discoveries each of which has implications in contemporary conservation biology.

First, Fran Hamerstrom detected a perturbation in the normal functioning system which she subsequently linked to the use of chemical contaminants, namely DDT. The ability to perceive an unhealthy disturbance in the system was directly related to the wide range of parameters measured in the study. For example, both harrier and microtine populations remained relatively high despite DDT applications,

yet aberrant behavior and low reproductive success in harriers indicated the system had changed (Hamerstrom 1969). Collaboration with colleagues led to the discovery that DDT was indeed responsible for the observed environmental disturbance. Thus, a broad information base, as developed by Hamerstrom, is useful for detecting environmental perturbations and providing a sound scientific basis for making management decisions.

Secondly, she recognized that the abundance of voles regulates the number of breeding harriers and determines their mating systems (Hamerstrom et al. 1985). In order to provide an evolutionary context for this phenomenon, Hamerstrom et al. (1985) examined theoretical models and found their data supported the polygyny threshold model of Verner and Willson (1966). Edwards (1989) reported that placing wildlife research into a theoretical framework is necessary to understand complex biological interactions. Similarly, Hamerstrom's approach provides a solid foundation on which to make future management decisions and highlights the importance of a system and process oriented approach to conservation problems.

GRASSLANDS AND PINNATED GROUSE

In the mid 1930s Frederick Hamerstrom Jr. joined a research program that was focused on developing a management plan to maintain huntable populations of Greater Prairie Chickens in Wisconsin. As the years progressed and prairie chicken habitat continued to disappear, Frederick Hamerstrom realized that the management plan might never provide a recipe for filling game bags with prairie chickens; however, he believed it could provide the key to saving the birds from extirpation in Wisconsin.

Like Leopold, the Hamerstroms believed that the importance of saving a species could not be measured in dollars. Indeed, Hamerstrom et al. (1957) explicitly stated that equal weight should be given to the value of hunting prairie chickens, observing them, and just knowing that they exist. Clearly this implies some intrinsic value associated with the preservation of the species. Even the value of hunting was not viewed by Frederick Hamerstrom as solely economic because he believed that much of what made people hunt had to do with the intangible "experience" it provided (F.N. Hamerstrom Jr. pers. comm.). Hamerstrom et al. (1957) further illustrated the influence of Leopold by reporting their belief that prairie chickens are valued by hunters and nonhunters alike

as part of Wisconsin's heritage. The prairie chicken, now considered to be a threatened species in Wisconsin (Wisconsin Department of Natural Resources 1989), continues to persist in the state's last stronghold. The progressive approach used by Hamerstrom et al. (1957) to preserve this bird received international recognition and resulted in a comprehensive guide to prairie chicken management in Wisconsin.

The Hamerstroms' approach to saving the prairie chicken was to develop a management plan based on extensive research of a range of interactions between the birds and their environment, including information on seasonal habitat use, food preferences, mating systems, productivity, survival, ecological landscape, hunting, diseases and parasites, predators, and weather. Thus, the final plan was holistic in its approach and was based on sound scientific evidence, whereby factors responsible for population declines were identified and prioritized. Ultimately, nesting and brood cover were identified as the weak links in the system with winter food as a lesser consideration.

The most innovative part of the plan was Hamerstrom's long-term solution proposing landscape-scale management. Specifically, a system of grassland reserves, providing the limiting nesting and brood cover, would be dispersed throughout the management area to maximize the effective range of the prairie chicken (Hamerstrom et al. 1957). Hamerstrom considered factors such as the distribution and interspersion of reserves, their size, number, cost, as well as the effects of their edges. The Hamerstrom team eventually recommended dispersed parcels of grasslands rather than one large reserve because previous research indicated prairie chickens were able to satisfy some of their requirements from existing farmland. Therefore, interspersing small grasslands which provided nesting and cover for brood rearing among existing farmland increased the total area of suitable habitat. Presently, the important question of whether reserves should consist of a single large block of land or several smaller blocks (SLOSS) is still debated among biologists (Jarvinen 1982, Soule and Simberloff 1986).

Are We on the Road to a Land Ethic?

The widespread recognition that both Frederick and Frances Hamerstrom received for their work testifies to the effectiveness of their approach. Why

then is "conservation biology" only now gaining widespread acceptance? The process of self-examination by the wildlife profession provides several clues. Following the establishment of The Society for Conservation Biology and the publication of its journal, Conservation Biology, a series of authors debated the need for a new professional group and examined the role of conservation biology relative to the more traditional profession of wildlife management (Temple et al. 1988, Anonymous 1989, Bolen 1989, Edwards 1989, Gavin 1989, Hunter 1989, Teer 1988, Wagner 1989). Wagner (1989) reported that wildlife is managed to satisfy social values, and there is a clear perception that the wildlife profession has not kept up with the changing expectations of society. Empirical evidence suggests that the wildlife profession has continued to concentrate on economically important species despite society's increasing insistence on protecting a broader range of wildlife, including endangered and nongame species (Slack and Silvy 1990). This in turn led to a void between the expectations of society and the direction of the wildlife profession that is currently being filled by the Society for Conservation Biology.

Society's perception of conservation issues is changing as evidenced by increased media coverage, environmental literature, and political and legal attention focussed on the environment. Communities and some states now have mandatory recycling laws and energy conservation programs. Environmental issues now appear regularly on the front page of newspapers, and are featured prominently in nonscientific publications. The amount of environmental literature available to scientists and conservationists has also increased as the number of environmental journals grew fiftyfold from 1970 to 1980 (Western 1989). In 1987, 49 nations signed a landmark agreement proposing ways to forestall continuing losses of stratosphere ozone (Western 1989). More recently a proposal put forth by the United Nations calls for strict international guidelines to maintain clean air and water throughout the globe (Wall Street Journal, 31 January 1992).

In 1949 Aldo Leopold predicted that until society became more ecologically conscious and moved towards what he termed a land ethic, his approach to conservation problems would not be successful (Leopold 1949). In light of the trends outlined above, I suggest that society is indeed moving towards a land ethic. As a result, I feel that our acceptance of the approach endorsed by contemporary conservation

biologists and their predecessors represents a corresponding lurch ahead.

ACKNOWLEDGMENTS

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RAPTOR CONSERVATION IN VERACRUZ, MEXICO

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Abstract.—This article presents aspects of raptor conservation, including training of local students, developing networks to monitor bird trade and to protect natural areas, establishing banding stations in Veracruz, ecotourism, and cooperative efforts among raptor biologists in North America and Veracruz. Because 67 raptor species are found in Veracruz, Mexico, and because the most northern high evergreen rainforest of the continent is located in this Mexican State, a major conservation effort in this region is certainly warranted.

Conservación de aves rapaces en Veracruz, México

Extracto.—Este artículo discute aspectos relacionados con la conservación de aves de presa; tales como el entrenamiento de estudiantes locales, el desarrollo de redes de vigilancia para el mercadeo de aves y la protección de áreas naturales, el establecimiento de estaciones de anillamiento, ecoturismo, así como la cooperación entre estudiosos de las aves de presa en Norteamérica y Veracruz. La necesidad de mayores esfuerzos conservacionistas en esta región se hace patente, si se considera que en este estado mexicano se encuentra la selva alta perennifolia más norteña del continente y tiene registradas sesenta y siete especies de aves de presa.

On 23 April 1990 I became a Hamerstrom "gabboon." During my four-month stay in Plainfield, Wisconsin I learned much about raptors from Frederick and Frances Hamerstrom. I especially enjoyed those times when we talked about their experiences with neotropical raptors in Los Tuxtlas, Veracruz, Mexico, and their interest in tropical forest conservation. The Hamerstroms believe that it is very important to support Latin American students in order to establish a group of individuals with an adequate level of expertise to develop effective conservation schemes in the Neotropics. Here, I return the favor of their training by writing about areas in the Neotropical forest of Veracruz, Mexico, where the Hamerstroms worked in the late sixties.

Study Area

The State of Veracruz, Mexico, extends from 17°10′N to 22°15′N, between the Gulf of Mexico to the East and the Mexican states of the Central Plateau to the West (Soto and García 1986). Elevation in the state ranges from sea level to 4300 m above sea level (Marchal 1984). Twenty vegetative types, including high evergreen rainforest, tropical deciduous forest, cloud forest, evergreen oak forest, marshes, mangrove swamps, brackish estuaries, beach communities and various forms of agricultural and grazing lands occur in the region. Eighty-five of 8000 plant species in the region are listed as endangered species (Dirzo 1987, Flores and Gerez 1988). Of the approximately 685 bird species recorded for the state (Loetscher 1941, 1955, Peterson and Chalif 1989, Schaldach pers. comm.), 137 are listed as endangered (Aguilar-Ortiz 1970, Ramos 1985, Vega 1988).

Historical View

The role of raptors was notable in the pre-hispanic cultures that flourished in Veracruz. The Olmecas and Totonacas erected sculptures representing several species of birds of prey (De la Fuente 1975, Medellín 1983). The agricultural and sylvicultural practices of the ancient residents of Veracruz apparently were compatible with their environment (Siemens 1981, 1982, Alcorn 1983).

An epidemic in the mid-15th century caused a decrease in the Indian population, thus permitting the Spaniards to take over Indian lands, at which time cattle ranching was promoted. Some Indians moved to the mountains, while others were assimilated. This situation, together with a massive immigration from Spain, imposed an incompatible resource management system that had been developed in the temperate regions of the Old World (Gunder 1982, Gómez-Pompa 1985).

As a result, the traditional knowledge of resource management in the area has been forgotten or lost. Consequently, for example, courses offered by the Universidad Veracruzana, colleges of Biology, Veterinary Science and Agronomy, today focus mainly on studies of exotic, rather than native, species, and cattle ranching is currently the predominant agricultural activity in Veracruz.

CURRENT PROBLEMS

Forest destruction promoted by agriculture and human colonization of tropical areas is the major threat to Neotropical raptors in Veracruz. Forest-dwelling birds have been greatly affected and their population sizes have decreased (Ramos 1985) by this factor. The extirpations of Harpy Eagles from Central Veracruz and Los Tuxtlas, King Vultures and Bicolored Hawks from Los Tuxtlas (Coates-Estrada and Estrada 1985, Iñigo et al. 1987, Aguilar in press a), as well as the proliferation in those areas of raptor species that favor disturbed habitats (Gómez 1991), constitute an example of habitat loss and alteration that applies also to other tropical areas in Mexico.

Raptors are often shot by farmers and hunters even when it is not permitted by law. Most of the hunters in Veracruz are not able to identify native species or to recognize scientific names in hunting calendars so that hunting regulations are rarely followed. Raptors are especially vulnerable to hunting during fall migration, when hunters seeking White-winged Doves (*Zenaida asiatica*) kill large numbers of birds of prey at El Viejón, Veracruz (R.S. Aguilar pers. comm.).

Pesticide pollution constitutes another threat. Albert et al. (1989) found organochlorine compounds in brain, liver and adipose tissue samples of an Ornate Hawk-Eagle from Santa Marta, in Los Tuxtlas, Veracruz. Additional research is needed to determine the impact of pesticides in raptor populations in this region.

Aguilar (in press b) found that in Xalapa, Veracruz, the Roadside Hawk, White-tailed Kite, Crested Caracara and the American Kestrel are frequently traded in local markets; during fall migration other species are trapped and sold in Mexico City (R.S. Aguilar pers. comm.).

COOPERATIVE RESEARCH AND
MANAGEMENT SCHEMES

Despite these problems Veracruz, Mexico, has 67 species of raptors (Table 1), and recent changes in the roles of local universities, together with a growing concern among the civilian population, offer hope.

Several institutions, including the Universidad Veracruzana (U.V.), the Universidad Nacional Autónoma de México (U.N.A.M.), the Instituto de Ecología A.C., the Instituto Veracruzano de Cultura (IVEC), and an emerging local ornithological so-

ciety, could play a major role in raptor conservation (Appendix 1).

Consider, for example, the Universidad Veracruzana. Every university in Mexico has a required undergraduate program called Servicio Social (Social Service), consisting of community service for one year. Much research, both basic and applied, could be accomplished by using this program to foster conservation efforts. Although students must work in a Mexican institution, researchers in North America can direct students and contribute to the establishment of successful conservation programs in Veracruz.

The Instituto Veracruzano de Cultura works mainly to maintain cultural traditions within the State of Veracruz. Several of its programs are concerned with the restoration of traditional methods of natural resource management. It is now realized that the conservation of natural diversity and social diversity go together. This institution has 57 Casas de Cultura (Culture Houses) throughout the State that offer logistic support for students working on their "Social Service."

Training of local people is important because the success of tropical forest conservation depends on local enthusiasm and participation. A major problem in this area is language. Few students in Veracruz speak English, and few American raptor biologists speak Spanish. One solution to this conundrum would be to have Latin American students spend several months interning in North America to allow them to learn English and to prepare them for future interactions with their northern colleagues. They would also then be available to teach Spanish to the North American counterparts.

Other, more advanced, students could begin graduate studies in North America if financial support were available. Upon their return to Latin America they wold form the nucleus of a local raptor group.

Raptor biologists visiting Latin America should offer to give talks or workshops to interested local inhabitants. Also, when North American scientists plan research projects in Latin America, they should hire local field assistants. Furthermore, many Mexican universities allow foreign advisers, enabling North American scientists to direct graduate students in Mexico.

Although protected areas in Veracruz cover 1% of the state (Flores and Gerez 1988), only at the Estación de Biología Tropical de Los Tuxtlas (U.N.A.M.) is there appreciable vigilance. For ex-

Table 1. Raptor species reported for Veracruz, Mexico.[1]

ENGLISH NAME	SPANISH NAME[2]	SCIENTIFIC NAME
Black Vulture b[3]	Carroñero común	*Coragyps atratus*
Turkey Vulture b	Aura común	*Cathartes aura*
Lesser Yellow Vulture	Aura sabanera	*Cathartes burrovianus*
King Vulture	Carroñero rey	*Sarcoramphus papa*
Osprey m	Aguila pescadora	*Pandion haliaetus*
Gray-headed Kite	Milano cabecigrís	*Leptodon cayanensis*
Hook-billed Kite	Milano piquiganchudo	*Chondrohierax uncinatus*
Swallow-tailed Kite m	Milano tijereta	*Elanoides forficatus*
White-tailed Kite	Milano coliblanco	*Elanus caeruleus*
Snail Kite	Milano caracolero	*Rostrhamus sociabilis*
Double-toothed Kite	Milano bidentado	*Harpagus bidentatus*
Mississippi Kite m	Milano migratorio	*Ictinia mississippiensis*
Plumbeous Kite	Milano plomizo	*Ictinia plumbea*
Bald Eagle r	Águila cabeciblanca	*Haliaeetus leucocephalus*
Northern Harrier m	Aguililla rastrera	*Circus cyaneus*
Sharp-shinned Hawk m	Gavilán pechirrufo menor	*Accipiter striatus*
Bicolored Hawk	Gavilán pechigris	*Accipiter bicolor*
Cooper's Hawk m	Gavilán pechirrufo mayor	*Accipiter cooperii*
Crane Hawk	Aguililla zancona	*Geranospiza caerulescens*
White Hawk	Aguililla blanca	*Leucopternis albicollis*
Common Black Hawk	Aguililla negra menor	*Buteogallus anthracinus*
Great Black Hawk	Aguililla negra mayor	*Buteogallus urubitinga*
Harris' Hawk	Aguililla rojinegra	*Parabuteo unicinctus*
Black-collared Hawk	Aguililla canela	*Busarellus nigricollis*
Solitary Eagle	Águila solitaria	*Harpyhaliaetus solitarius*
Gray Hawk	Aguililla gris	*Buteo nitidus*
Roadside Hawk	Aguililla caminera	*Buteo magnirostris*
Red-shouldered Hawk b	Aguililla pechirrojiza	*Buteo lineatus*
Broad-winged Hawk m	Aguililla migratoria menor	*Buteo platypterus*
Short-tailed Hawk	Aguililla braquiura	*Buteo brachyurus*
Swainson's Hawk m	Aguililla migratoria mayor	*Buteo swainsoni*
White-tailed Hawk	Aguililla coliblanca	*Buteo albicaudatus*
Zone-tailed Hawk	Aguililla aura	*Buteo albonotatus*
Red-tailed Hawk	Aguililla colirrufa	*Buteo jamaicensis*
Harpy Eagle	Aguililla Harpía	*Harpia harpyja*
Black-and-White Hawk-Eagle	Aguililla vientriblanca	*Spizastur melanoleucus*
Black Hawk-Eagle	Águila tirana	*Spizaetus tyrannus*
Ornate Hawk-Eagle	Águila elegante	*Spizaetus ornatus*
Red-throated Caracara u	Caracara comecacao	*Daptrius americanus*
Crested Caracara	Caracara común	*Polyborus plancus*
Laughing Falcon	Halcón guaco	*Herpetotheres cachinnans*
Barred Forest-Falcon	Halcón selvático menor	*Micrastur ruficollis*
Collared Forest-Falcon	Halcón selvático mayor	*Micrastur semitorquatus*
American Kestrel b	Halcón cernícalo	*Falco sparverius*
Merlin m	Halcón esmerejón	*Falco columbarius*
Aplomado Falcon	Halcón fajado	*Falco femoralis*
Bat Falcon	Halcón enano	*Falco rufigularis*
Orange-breasted Falcon	Halcón pechicanelo selvático	*Falco deiroleucus*
Peregrine Falcon m	Halcón peregrino	*Falco peregrinus*
Prairie Falcon m	Halcón pálido	*Falco mexicanus*
Barn Owl	Lechuza de campanario	*Tyto alba*

Table 1. Continued.

ENGLISH NAME	SPANISH NAME[2]	SCIENTIFIC NAME
Flammulated Owl	Tecolote ojioscuro serrano	*Otus flammeolus*
Whiskered Screech-Owl	Tecolote rítmico	*Otus trichopsis*
Vermiculated Screech-Owl	Tecolote crescendo	*Otus guatemalae*
Crested Owl	Búho corniblanco	*Lophostrix cristata*
Spectacled Owl	Búho gorjiblanco	*Pulsatrix perspicillata*
Great Horned Owl	Búho cornado americano	*Bubo virginianus*
Least Pygmy-Owl	Tecolotito menor	*Glaucidium minutissimum*
Ferruginous Pgymy-Owl	Tecolotito bajeño	*Glaucidium brasilianum*
Burrowing Owl	Tecolote zancón	*Athene cunicularia*
Mottled Owl	Búho tropical	*Ciccaba virgata*
Black-and-White Owl	Búho blanquinegro	*Ciccaba nigrolineata*
Barred Owl	Búho serrano ventriblanco	*Strix varia*
Stygian Owl	Búho cornado oscuro	*Asio stygius*
Striped Owl	Búho cornado cariblanco	*Asio clamator*
Short-eared Owl m	Búho cornicorto llanero	*Asio flammeus*
Northern Saw-Whet Owl	Tecolote abetero norteño	*Aegolius acadicus*

[1] From Peterson and Chalif (1989), Schaldach (pers. comm.), Sada et al. (1987), Loetscher (1941, 1955), and Lowery and Dalquest (1951).

[2] Spanish names vary within the State. The names used here should be considered as a reference.

[3] Letters refer to population status: b = migratory and resident populations; m = migratory; r = rare winter visitor; u = uncertain numbers, unlettered species are residents.

ample, the rainforest in the San Martín and Santa Marta volcanoes, and the Uxpanapa region, are in urgent need of protection since their fragmentation is affecting forest dwelling raptors. A local committee should develop a network to alert northern colleagues about the situation of these areas, and other issues, including the bird trade, such a committee should inform local authorities and decisionmakers.

During spring migration more than 250 000 raptors have been recorded passing through Veracruz (Thiollay 1980, Tilly et al. 1990). Hawk Mountain Sanctuary Association, Hawk Watch International, and the Mexican group Ecosfera are currently studying migration in Veracruz. Funding for research, monitoring, and education remains a major problem, and today there are few opportunities to work as a biologist in Veracruz.

Ecotourism in Veracruz is an exciting prospect because of the multitude of bird species and the varied vegetative types. These attributes, together with more than 40 archaeological sites (Winfield 1991), make Veracruz a natural site for the development of this type of conservation effort.

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SHORT COMMUNICATIONS

EYE COLOR OF COOPER'S HAWKS
BREEDING IN WISCONSIN

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Several authors have noted the progressive changes in eye color with age in North American accipiters (Grossman and Hamlet 1964, Meng 1951, Snyder and Snyder 1974). These changes are believed to proceed from shades of yellow in younger birds to shades of orange or red in older birds. Snyder and Snyder (1974) suggested that these changes in eye color are also associated with gender and speculated about the function of eye color. Here we use the eye color recorded during 377 captures of breeding Cooper's Hawks (*Accipiter cooperii*) in Wisconsin (1980–91) to examine eye color in relation to age and gender. We also discuss our results in relation to breeding quality in males.

STUDY AREA AND METHODS

We trapped breeding Cooper's Hawks at 105 separate nesting areas (Rosenfield and Bielefeldt 1992) throughout Wisconsin during 1980–91. We caught 253 different individuals (113 males and 140 females) and retrapped some of the same birds a total of 124 times in subsequent years. Most Cooper's Hawks were trapped near their nests in mist nets (3 × 12 m) using a live Great-Horned Owl (*Bubo virginianus*) as a decoy (Hamerstrom 1963). We also caught hawks in bow nets baited with European Starlings (*Sturnus vulgaris*) and Ring Doves (*Streptopelia risoria*).

Forty-two captures involved birds of known age: 1 yr old individuals in predominantly brown plumage (*N* = 17); 2 yr old individuals (all males) with two generations of gray feathers, plus a few retained brown feathers on rump and/or scapular areas (*N* = 4); 2 or 3 yr old individuals originally marked as nestlings (Rosenfield and Bielefeldt 1992; *N* = 5); and 16 recaptures of the above individuals in later years. The remaining 335 captures involved 227 individuals of unknown initial age (ASY birds ≥2 yr of age) and 108 recaptures of these individuals (A3Y, A4Y, etc.) in subsequent years.

Captures of males at a given nesting area are also divided between the initial individual trapped on an area (*N* = 82) and subsequent individuals (replacement males) trapped on the same area in later years (*N* = 31). We assumed that eye colors in our sample of initial male individuals on these 82 different nesting areas represented the actual proportion of various eye colors within the breeding population in Wisconsin.

We determined the predominant color over the major part of the iris using the following categories in the color chart in Palmer (1962): yellow, orange-yellow, orange, scarlet-orange, and scarlet. Hereafter we regard orange-yellow, scarlet-orange, and scarlet as light orange, dark orange, and red color categories, respectively. In calculat-

Table 1. Iris color of known-age Cooper's Hawks breeding in Wisconsin.

AGE IN YEARS	EYE COLOR CATEGORIES				
	YELLOW	LIGHT ORANGE	ORANGE	DARK ORANGE	RED
Males (*N* = 29 captures)					
1	2	8	0	0	0
2	0	3	5	0	0
3	0	2	3	1	0
4	0	0	2	2	0
5	0	0	0	0	1
Females (*N* = 13 captures)					
1	6	1	0	0	0
2	0	2	0	0	0
3	0	1	0	0	0
4	1	0	1	0	0
5	0	0	0	1	0

Table 2. Iris color of "relative-age" Cooper's Hawks breeding in Wisconsin. Relative-age birds are after second year birds (ASY), and recaptures of these individuals (A3Y, A4Y, etc.) in subsequent years.

	EYE COLOR CATEGORIES						MEAN EYE COLOR SCORE
RELATIVE AGE	1 YELLOW	2 LIGHT ORANGE	3 ORANGE	4 DARK ORANGE	5 RED	TOTAL	
Males (N = 155 captures)							
ASY	0	14	37	26	19	96	3.5
A3Y	0	1	13	18	4	36	3.7
A4Y	0	0	4	5	6	15	4.1
A5Y	0	0	0	1	4	5	4.8
A6Y	0	0	0	0	2	2	4.7
A7Y	0	0	0	1	0	1	
Females (N = 180 captures)							
ASY	7	43	58	21	2	131	2.8
A3Y	0	7	12	4	1	24	3.0
A4Y	0	3	4	2	1	10	3.1
A5Y	0	0	5	2	0	7	3.3
A6Y	0	0	5	1	0	6	3.3
A7Y	0	0	1	1	0	2	

ing mean eye color scores for hawks in a given age category, we assigned corresponding numerical scores of 1–5 for yellow through red eyes, respectively. Clutch size was determined in 1980–91 by climbing to nests in mid-late incubation (typically about mid-May in Wisconsin).

RESULTS AND DISCUSSION

In both sexes eye color showed a progressive change from lighter shades of yellow in younger birds to darker shades of orange or red in older birds (Tables 1, 2). However, 1 yr old males had significantly darker eyes, usually light orange, than 1 yr old females did, which are usually yellow ($\chi^2 = 6.51, P < 0.05$). Although our data on females did not allow further statistical comparisons of eye color between the sexes for known-age hawks, at relative ages from ASY through A7Y males always showed a markedly higher mean eye color score than females of the same relative age (Table 2). Thus the initial gender disparity in eye color in yearling hawks not only persisted in older birds, but also increased with relative age (Table 2).

Males that were 2–5 yr old were very unlikely to have yellow eyes, while males that were 4–5 yr old were not likely to have light orange eyes. Conversely, it seemed that most males did not attain their red eyes until ≥ 5 yr of age.

In both sexes, detectable changes in eye color appeared to cease once the birds were about 5 yr old (Table 2). Asymptotes seem to occur at the same relative age for both sexes, but females reached their asymptote at markedly lower scores than did males (3.3 vs. 4.7; Table 2). Evidently, some females did not achieve red eyes, at least at ages up to A7Y.

Our data on male ages and eye colors were also useful in examining the possibility that preferential mating occurs on the basis of eye color in males, as suggested by Snyder and Snyder (1974). Our information from ASY captures suggests that about 20% of breeding male Cooper's Hawks in Wisconsin had red eyes (Table 2). However, this sample of ASY birds may have been skewed toward males with lighter eyes because it included replacement males at some nesting areas; such replacements could predominantly have been younger males with lighter eyes. We thus compared eye color in individual males initially captured on 82 nesting areas with eye color in

Table 3. Iris color of initial and replacement male Cooper's Hawks at 82 nesting areas in Wisconsin.

	EYE COLOR CATEGORIES						MEAN EYE COLOR SCORE
	1 YELLOW	2 LIGHT ORANGE	3 ORANGE	4 DARK ORANGE	5 RED	TOTAL	
INITIAL	1	18	24	21	18	82	3.5
REPLACEMENT	1	7	17	5	1	31	2.9

Table 4. Clutch size by eye color category for breeding male Cooper's Hawks in Wisconsin.

COLOR CATEGORY	N	$\bar{x}$	RANGE
Yellow	1	4.0	NA
Light Orange	12	4.25	3–6
Orange	45	4.40	2–5
Dark Orange	28	4.28	2–6
Red	19	4.68	4–5

replacement males at 31 of these areas. Initial males did show a greater proportion of red eyes than replacement males (22% vs. 3%) and initial males had higher mean eye color scores than their replacements (Table 3). Therefore, we regard the 22% figure as the actual proportion of red-eyed males in the breeding population.

Snyder and Snyder (1974) hypothesized that red eyes "could be a good indicator" of the age and quality of a male and that "hunting skills may improve progressively over the lifetime of a bird." They postulated that birds with the darkest red eyes might have the greatest success in obtaining mates. If older, darker-eyed males are indeed higher quality mates and more proficient hunters than younger, lighter-eyed males, there should be fitness differences related to eye color.

We suggest that a revealing test of male quality should be clutch size. Males provide virtually all the food to their mates in the pre-incubation period (Rosenfield et al. 1991), a time in which both prey abundance and vulnerability are presumably at their lowest levels during the breeding cycle. This role as principal supplier of prey, as well as the males' relative hunting skills in the pre-incubation period, should be manifest in the pair's clutch size. Although males with red eyes had the largest mean clutch size (Table 4), there was no statistically significant difference in clutch size among the eye color categories (median test $\chi^2 = 5.02$, df = 3, $P > 0.05$). Therefore we found no support for the premise that male fitness is associated with male eye color. Finally, if the darkest red eyes were associated with male quality, we could expect selection for a proportion of red-eyed males much higher than the 22% we found in the Wisconsin breeding population.

RESUMEN.—Hemos examinado las relaciones entre edad, sexo, vigor de los machos (i.e., número de huevos en el nido), y el color de los ojos, en 253 gavilanes de la especie *Accipiter cooperii*, durante el ciclo de reproducción, en Wisconsin, desde 1980 a 1991. En ambos sexos el color de los ojos mostró un cambio progresivo que va del amarillo claro, en gavilanes jóvenes, al anaranjado obscuro ó al rojo, en aves de más edad. Los machos tuvieron ojos más obscuros que las hembras de la misma edad. No hemos encontrado justificación a la hipótesis que sostiene que el vigor de los machos está asociado con el color de los ojos. No hubo diferencias en los tamaños de las nidadas que estuvieran en relación con categorías en el color de los ojos.

[Traducción de Eudoxio Paredes-Ruiz]

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The Influence of Gender and Hatching Order on Growth in Hen Harriers (*Circus cyaneus cyaneus*)

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The sexual dimorphism of adult Hen Harriers (*Circus cyaneus cyaneus*) was described and compared to other European harriers by Nieboer (1973). Scharf and Hamerstrom (1975) and Picozzi (1982) describe adult sexual dimorphism in live, wild-caught populations comparing Hen Harriers with Northern Harriers (*C. c. hudsonius*). The ontogeny of sexual dimorphism and growth of Hen Harrier nestlings identified by sex has been described in Orkney, Scotland (Scharf and Balfour 1971, Picozzi 1980). Divergence of growth rates as well as differences in tarsus size and eye color between the sexes can be detected as early as 10 d after hatching in this species (Hamerstrom 1968, Scharf and Balfour 1971).

The asynchronous hatching of harriers results in young of different sizes. Female nestlings are always larger in mass and primary feather length than males of the same age from 10 d after hatching. Scharf and Balfour (1971) state that nestlings of either sex did not change their position in the size hierarchy created by their hatching sequence. A change in nestling rank might be expected if younger females grew fast enough to overcome the size of an older male nest mate. Occasionally, pairs produced nestlings of closer ages than usual because their eggs hatched at intervals of less than 48 hr (Balfour 1957). However, even in those cases, there was no change in relative sizes among nestlings (Scharf and Balfour 1971). Picozzi (1980) cites several nests with up to four nestlings hatching on the same day, but still retaining the initial size hierarchy. In this paper, I quantify similarities in the development of dimorphism through differential growth in each sex and the differences between growth rates in hatching order.

Study Area and Methods

The Orkney Islands are 12 km north of the Scottish mainland at latitude 59°N. Edward Balfour helped me find 38 nests in 1967 and 42 nests in 1968 in his 80 km² moorland study area. I weighed and measured a total of 144 harrier nestlings combining 26 nests in 1967 with 24 nests in 1968. This analysis is limited to a subset of 59 first and second hatched nestlings from 31 of those nests. The nestlings were measured for mass and primary length as close as possible to 1 d intervals. This was feasible because of the absence of mammalian and reptilian predators in Orkney. Visits to nests were done quickly to minimize disturbance. Both adults and nestlings tolerated my presence well, and no nest desertions were attributed to my activities at the nests.

The composite sample analyzed here consists of 317 mass, and 286 linear measurements of the longest primary (the 6th primary, counted from inner to outer; Ashmole et al. 1961). The sample sizes reported here are smaller than those of Scharf and Balfour (1971), because I limited this analysis to the first and second hatched nestlings (A and B nestlings respectively). Twenty-four nestlings were found either while hatching or while still wet. Older nestlings were assigned age by back-dating from the normal hatching interval. Ages used here are believed accurate within 24 hr. All nestlings were assigned as to sex after day ten and before they left the nest, using the method of Hamerstrom (1968). For further information on the methods of marking, weighing, measuring, and recording, see Scharf and Balfour (1971).

Only nestlings that appeared healthy are used in this analysis. Nestlings which subsequently died were excluded. Linear regression analysis was used to compare growth rates (Lyons and Mosher 1983, Steidel and Griffin 1991). The regressions are calculated for mass and longest primary by sex and rank for the following four classes: A and B females and A and B males. I then compared the growth of each sex of A nestlings to the growth of each sex of B nestlings (Zar 1974). By doing this, I propose to separate the effects of gender-specific growth rates from the possible acceleration or depression of growth rate due to hatching order.

Growth data reported here are of the mixed longitudinal type in which a composite of measurements repeated from different individuals may not represent or extend over the full range of ages that were recorded (Cock 1966).

Results

Annual Variation. To assess the possibility of differences in growth between years due to differences in food abundance, weather and other extrinsic factors, I compared the mass of both sexes of A and B nestlings for each year. Mass was chosen because it is a more environmentally sensitive measure (Scharf and Balfour 1971). Linear regressions calculated from nestling mass were not significantly different within the sexes and hatching order for the two years (A-females, $t = 0.86$, $df = 111$; A-males, $t = 1.74$, $df = 68$; B-females, $t = 1.30$, $df = 56$; B-males, $t = 1.11$, $df = 74$; $P > 0.10$). Based on the similarity of these results between years, data from both years are combined in the following analyses.

Gender and Growth. The mass and feather growth rates of females were significantly greater and extended over a greater time span than those of males in both A and B chicks (Table 1). Males fledged somewhat earlier

Table 1. Mass (58–113 measurements) and longest primary feather (62–98 measurements) growth rates for 59 nestling Hen Harriers.

RANK	SEX	N	MASS				PRIMARY			
			MEASUREMENTS	g/DAY[1]	SE	r^2	MEASUREMENTS	mm/DAY	SE	r^2
A	F	20	113	16.4A	±0.6	0.93	98	8.1A	+0.1	0.98
A	M	13	70	13.0B	±0.6	0.94	62	7.4B	+0.2	0.98
B	F	13	58	19.2C	±0.7	0.96	64	8.1A	+0.2	0.99
B	M	13	76	12.6B	±0.7	0.90	62	7.1C	±0.3	0.96

[1] Means with different letters are significantly different ($P < 0.001$); those with same letters are not ($P > 0.05$).

than females. Primary feather growth and mass gain of males slowed markedly after day 30. Males achieved a wing loading which allowed them to fly as much as 4 d before their female counterparts (31–34 vs. 35–38 days at first flight; Scharf and Balfour 1971). Mass at fledging showed roughly the same 30% difference between the sexes as when the fledglings were adult during the breeding season. Adult dimensions in mass and primary are not reached until several months after fledging (Scharf and Balfour 1971). Female primary lengths, however, had their greatest margin over males at fledging, and the difference decreased with age (16% longer in fledglings, but only 13% longer in adults; Scharf and Balfour 1971).

Hatching Order and Growth. Differences in mass according to ranks and sex are given in Table 1. The rates are significantly different between A females and A males, B females and B males. The A females had a daily gain of 16.4 g/day compared to 19.2 g/day for B females. However, the A male and B male comparisons of growth rates in mass showed no significant difference.

Feather growth (Table 1) was significantly different between the A female and A male, B female and B male, and the A male and B male but not the A female and the B female (Table 1). This was the reverse of the comparisons of the A female and B female for the mass growth rates given above.

DISCUSSION

My results showed that differences in growth rates in Hen Harriers are determined primarily by the sex of the nestling. Hatching order also influenced mass gain in A and B females, and the rate of primary feather growth in A and B males. The evidence that females exhibit faster growth than males is counter to Olendorff's (1971) findings in buteos. Even though the female grows faster in Hen Harriers, females spend more time in the nest, and males may benefit by being able to leave the nest sooner. I hypothesize that earlier fledging by male harriers may have contributed to the similar growth rates in mass between A males and B males. The later development of primary feathers in females, shown by the similarity of primary growth rates between A and B females, is one factor causing females to reach higher weights and stay in the nest longer before reaching the wing-loading which enables flight.

Steidel and Griffin (1991) showed that growth in Ospreys (*Pandion haliaetus*) was not affected by hatching

order and, further, that growth was not influenced by brood reduction. The relative constancy of growth in the sexes and hatching orders of Hen Harriers in this study counters the probability of size-influenced brood reduction as a cause of the skewed sex ratios in Hen Harriers reported by Balfour and Cadbury (1979). The growth rates described here for Hen Harriers is in marked contrast to that in Bald Eagles (*Haliaeetus leucocephalus*) and Golden Eagles (*Aquila chrysaetos*) where the difference in mass between siblings depends on the degree of hatching asynchrony and size differences between the sexes can be inflated through nestling competition and even siblicide (Bortolotti 1986, Edwards and Collopy 1983). It is possible that my results were influenced by 1) data collected during two "good" food years and 2) size related mortality being possibly greater in the C, D, or E nestlings (Picozzi 1980).

Ricklefs (1983) divides the factors responsible for variation in growth rates into environmental (including food availability and sibling competition), parental effort, and the anatomical and physiological constraints to growth, which are genetically determined. My data on growth in Hen Harriers show a greater similarity of growth within sex and hatching order than may be expected and point toward the anatomical and physiological constraints as the prime determinants of Hen Harrier growth.

RESUMEN.—El peso y la medida de la pluma primaria más larga de 59 raptoras de la especie *Circus cyaneus cyaneus*, mientras permanecían en el nido, son analizados por regresión en 31 nidos. Así se establece el grado de crecimiento para aves jóvenes A y B de cada sexo. Haciendo esto, cuantifico la ontogenia del dimorfismo sexual a través del crecimiento diferencial. Las primeras y segundas crías de la nidada crecen en proporciones relativamente fijas dentro de cada sexo. Las crías hembras permanecen más tiempo en el nido y alcanzan más peso y longitud de plumas antes de volar; ellas comienzan a divergir anatómicamente hacia el décimo día después de nacer, y tienen una medida de crecimiento más alta que los machos. Los resultados muestran significativas diferencias para el aumento de peso entre las primeras y segundas crías hembras; y para el crecimiento de las plumas primarias entre las primeras y segundas crías machos. Las primeras y segundas crías machos no son significativamente diferentes en cuanto a peso; mientras que las primeras y segundas crías hembras no son significativamente diferentes en cuanto al crecimiento de las plumas primarias. Por tanto, la influencia

del sexo en la medida del crecimiento es una determinante primordial y está relacionada a constreñimientos fisiológicos y a la anatomía heredada en esta especie.

[Traducción de Eudoxio Paredes-Ruiz]

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LETTERS

AMERICAN KESTRELS (*Falco sparverius*) ADOPT AND FLEDGE EUROPEAN STARLINGS (*Sturnus vulgaris*)

*Frederick Hamerstrom often lamented about how the current state of science does not allow an investigator to deviate from his/her pre-planned protocol. His view was that unusual and interesting "side events" often were overlooked because time and money did not allow for such "unnecessary" investigations. In memory of Hammy, we present an unplanned study of a truly unusual event: the adoption of and eventual fledging of a brood of European Starling (*Sturnus vulgaris*) chicks by a pair of American Kestrels (*Falco sparverius*).*

In 1968 we placed 50 kestrel nest boxes on our 20 243 ha study area in central Wisconsin (F. Hamerstrom et al. 1973, *J. Wildl. Manage.* 37:400–403). An average of over 50 boxes has been maintained through 1990. In 1988 we started an intensive study and checked the boxes weekly during the breeding season. We caught and identified or banded any adults, and took notes.

In April 1988 we caught a pair of kestrels in the Rosen box. This pair initially had six eggs, but by 20 May only four eggs remained. On 24 May we found four young about 2–3 d old in the box. Four days later (28 May) the young had disappeared. There were scratches on the side of the box, which suggested predation by a mammal.

On 28 May the West Brandt box, 1.1 km from the Rosen box, contained six young European Starlings. Of these, four appeared to be dead, one dying, and one "still cheeping." By 0730 H we had caught the Rosen male kestrel on a *bal-chatri* near the West Brandt box and the Rosen female inside the box.

From the field notes: "May 28. Watch box [West Brandt] 0845–1045 H. Starlings fly to box about every 15 minutes with food [earthworms] in bill, but do not enter. If a starling flew in while the kestrels were out of the box, both male and female kestrel chased the starlings away.

June 3, 0550 H. Same banded female caught on five starling young. Female missing crown feathers. Left eye swollen and glassy. Perhaps wounds on head are from starling gapes?

June 3, 1545–1800 H. See male and female kestrel hanging in nest hole. Young starlings open gapes and crowd to hole. Kestrels appear to be placing small prey in starling gapes, but we couldn't see any prey. Male flew to perch near box with small, green, thin snake. Female perches next to male and then takes snake into box. Female kestrel stays in box about 10 min. Female catches mouse, brings it into box and stays ±15 min. Can see waving gapes while female kestrel is in the box, but not female feeding them. At 1800 H, check box. No signs of snake or mouse there! Female overhead circling.

June 4, 0600–0900 H. Set blind 38 m and second observer ±61 m from box. Female enters box with mouse but leaves after ±1 min with mouse. ±20 min later, female enters box with mouse—tears small pieces of mouse and places them in gapes of young starlings who lunge forward and place entire gape around female kestrel's head! Female kestrel feeds starling 2 more mice. Female [kestrel] mobbed by both adult starlings. One [starling] perches and hops toward box, female kestrel chases it.

June 5, 0600–1100 H. Female kestrel feeds starlings 4 mice—again starling gapes envelope female kestrel's head. Adult starling perches on top of and near hole of box. Kestrels not near. Starling leaves. Starling young call to adult starling, but more [vigorously] to approaching kestrels!"

[Note: every time the robins nesting nearby saw a kestrel coming back to the nest, usually with prey, they gave loud alarm calls—calls that the young starlings soon recognized as a "dinner bell." They responded by sticking their heads out of the nest box and waving their big, yellow gapes.]

"June 6, 0640–0820 H. ±0745 female kestrel lands near box with a partially skinned mouse—some fur on its back legs. She flushes three times before entering the box [perhaps to avoid further injury to her eye]. Finally she goes into the box and feeds the young for 18 minutes."

We saw two of the young starlings fledge; one flew 14 paces on its first flight. By 9 June the box was empty.

We have recorded the following on video: a female kestrel bringing food to the box and hanging on the entrance; the eager response of the starlings to approaching kestrels and their unusual indifference to adult starlings even when these entered the box; the female kestrel tearing slender, green snakes and voles, and placing the morsels in the starlings' mouths; and one starling fledging over the female kestrel's back.

We are deeply indebted to Hammy for his insatiable curiosity, and his interest in science. Ruth L. Hine and Jennifer A. Leak assisted in field observations.—**Michael F. Tlusty, Department of Biology, Syracuse University, Syracuse, NY 13244 and Frances Hamerstrom, College of Natural Resources, University of Wisconsin–Stevens Point, Stevens Point, WI 54481.**

NORTHWARD MIGRATION OF AN ADULT NORTHERN HARRIER (*Circus cyaneus*)

A nesting male Northern Harrier (*Circus cyaneus*) banded in San Diego, California (32°30'N 116°50'E) was found dead near Klamath Falls, Oregon (42°00'N 121°40'E) 47 d later, a straight line distance of 1175 km. Assuming the carcass was 7 d old (B. Waterbury pers. comm.) and that the harrier followed the most direct path northward, the average daily flight would have been a minimum of 29 km. Harriers are known to migrate south into San Diego County during the fall (P. Unitt 1984, The Birds of San Diego County, Memoir No. 13, San Diego Society of Natural History, San Diego, CA). Recent band recoveries indicate that juveniles may disperse northward to cooler climates (P.H. Bloom pers. comm.) as has been demonstrated for juvenile Bald Eagles (W.G. Hunt et al. 1992, *J. Raptor Res.* 26:19-23). Similar movements by adults have not been documented.

A pair of Northern Harriers was first detected in the lower Otay River Valley, 4 km north of the Mexican border on 8 April 1991, when a male was observed transferring food to a female. On 6 May, a nest was found in a dense stand of Black Mustard (*Brassica nigra*) on the south-facing slope of the river valley. It contained one egg and four young, the oldest young was estimated at 5-7 d of age (M.B. Saunders and G.L. Hansen 1989, *Can. J. Zool.* 67:1824-1827). Using minimum estimates of one egg hatching each day and a 31 d incubation period (F. Hamerstrom 1969, Pages 367-383 *in* J.J. Hickey [ED.], Peregrine Falcon populations: their biology and decline, University of Wisconsin Press, Madison, WI) the nest initiation date was estimated to be on or before 1 April, the earliest recorded in San Diego County (P. Unitt 1984, op. cit.). On 11 May, the female was brooding three young with no additional eggs in the nest suggesting either partial nest predation, cannibalism, or that the egg or small young had died and was removed from the nest by the parent.

The male harrier was trapped at 0800 H on 12 May 1991, 15 m from its nest using a *dho-gaza* trap with a juvenile Red-tailed Hawk (*Buteo jamaicensis*) as a lure (F. Hamerstrom 1963, *Proc. Int. Ornithol. Congr.* 13:866-869). The following measurements were taken: weight 365 grams, wing chord 340 mm, tail length 196 mm and tarsus length 793 mm. The bird was fitted with a color band and a U.S. Fish and Wildlife Service lock-on metal band on the right leg, and two color bands on the left leg. An 11 g tail mounted transmitter (AVM Electronics Inc., Livermore, CA) was attached to the number one and number two right rectrices using nylon ties and cyanoacetate glue. Total handling time was approximately 40 min.

The nest was checked again on 13 May and contained three young with both adults in attendance. The male harrier was last detected in the nesting area on 16 May 1991. On that date the female was perched near the nest while the male, initially located using telemetry, was hunting away from the nest for approximately 2 hr. A final check on 23 May revealed no juvenile or adult harriers in the vicinity of the nest and the three young were presumed to have been preyed upon. There was no evidence of intrusion by ground predators, however Red-tailed Hawks and Great Horned Owls (*Bubo virginianus*) were nesting in close proximity.

On 27 June 1991, the male harrier was found dead 11 km southeast of Klamath Falls, Oregon and taken to the Oregon Department of Fish and Wildlife. The bird was reported to be in deteriorated condition, dried out and picked clean by insects. It was estimated to have been dead a minimum of 1-2 wk. No cause of death could be determined. The bands were intact but the transmitter and the two tail feathers to which it was attached were missing.

—**Mark A. Pavelka, Ogden Environmental and Energy Services, 5510 Morehouse Drive, San Diego, CA 92121; John K. Konecny, 1141 Morning View Drive #208, Escondido, CA 92026; Kristine L. Preston and Mary A. Grishaver, Ogden Environmental and Energy Services, 5510 Morehouse Drive, San Diego, CA 92121.**

ON THE ETYMOLOGY OF THE NAME *Bal-Chatri*

The *bal-chatri* (pronounced ball chat-ree) is a trap used widely to capture birds of prey for banding, thanks to the descriptions given by D.D. Berger and H.C. Mueller (1959, *Bird Banding* 30:18-26). Various modifications have been reported by other authors (e.g., D.D. Berger and F. Hamerstrom 1962, *J. Wildl. Manage.* 26:203-206; W.S. Clark 1967, *Eastern Bird Banding Assoc. News* 30:147-149).

Berger and Mueller (1959, op. cit.) mention that this trap was developed and used in India many years ago and that, according to F. Craighead and J. Craighead (1942, *Nat. Geog.* 81:247), the name *bal-chatri* means boy's umbrella.

I was recently in India teaching raptor capture techniques to Indian biologists. As the translation given above did not make much sense to me, I asked my Indian colleagues what the name *bal-chatri* means. The answer given was very logical. *Chatri* indeed means umbrella in Hindi (and most of the related languages spoken in northern India), but *bal* means hair, especially horse hair. When I inquired further, I found that it could also mean boy. The original

traps were cane baskets with horse hair nooses affixed; the baskets were shaped somewhat like umbrellas. So, it would appear that the most appropriate translation of *bal-chatri* is horse-hair umbrella. This translation does make sense and is the one that should be used.—**William S. Clark, 4554 Shetland Green Road, Alexandria, VA 22312.**

"GABBOONING" IN PLAINFIELD

How does one become a gabboon? I quote one of Fran Hamerstrom's letters concerning my application to be one: "I have many questions: Is the applicant healthy? Does she eat special food? Is she strong enough to carry a light ladder and climb up to the nest boxes to pull out the falcons to band them etc.? Has she ever taken care of any animals? Wild pets? Other? Has she a driver's license? Does she mind working alone? What does she want to do with her life after she finishes her studies? The research is fascinating, but hard work. Getting up early, heat, mosquitoes, nettles."

Reflecting on these questions and with no inkling of what awaited me, I sat on a bus to Madison, Wisconsin, in April of 1989. The permission to work for the Hamerstroms had reached me in Germany only 10 d earlier. After a 22-hr journey, I was welcomed by Fran and Hammy in Madison—with slight reservation. Immigration technicalities had caused me to be 4 hr late! We set off without further delay for Plainfield. All three of us had probably envisaged a smoother start to our three-month stint of working together on the "kestrel project"—with fewer mishaps and less tension. Nonetheless, we noted with relief that our plans had been realized. On the way to Plainfield, Fran began telling me, in her direct way, that my work would earn me free board and lodging, but that "such things as lipstick you must pay for out of your own pocket." I was just able to mumble that my need of cosmetics was not overwhelming, before falling fast asleep for the rest of the 2-hr drive.

We arrived outside of Plainfield, at this ancient, crooked and at first glance rather chaotic house, in the middle of the night. In a trance, I followed Fran to my room with one thing in mind—more sleep! As I lay on the bed, still rather dazed from the journey, and stared at the unpretentious surroundings and the cracks in wall and ceiling, I thought I would never be able to stay the course—a verdict which was soon overthrown.

The world, next morning, had improved enormously. The sun shone on a wonderful countryside and, after a short "scenic tour" of the enormous Hamerstrom estate, my initiation started—not with fieldwork, but with a reading by Fran from one of her books.

Without loss of time I was confronted by one of the Hamerstroms' guiding principles: research and public service Much has been written about their contributions to the former, and with this issue of the *Journal of Raptor Research* more honors will be added. But the engagement of the Hamerstroms in public service, and their ability to stir enthusiasm for nature in one and all, cannot be overstated. Nowadays it is more important than ever to sponsor interest in our environment. For decades, Fran and Hammy have contributed to this effort enormously, not only with their lectures and books, but with their "gabboon system."

What is this enigmatic-sounding helper system? In fact it is no great secret. Quite simply, it consists of engaging people of all ages, but principally youngsters, as scientific workers, in which a lack of training is no hindrance. As for "gabboon"—the word stems from an African expression for slave. One quickly learns the essentials for efficient work, for instance distinguishing male raptors from females, banding the birds and writing field notes. Especially in more recent years, nearly all the fieldwork has been undertaken by the gabboons.

As I was fresh out of school, the amount of responsibility given me and the freedom in conducting fieldwork were fascinating. I have since learned to value this all the more, having spent 2.5 years at German universities, interacting with sometimes condescending professors.

Ever since the prairie chicken project, it was necessary for the Hamerstroms to trust their helpers completely, to give them responsible jobs, and to keep explanations and instructions to a minimum. Two persons (not even Fran and Hammy) cannot be everywhere on the booming grounds at all times! As a result, through the years over 7000 helpers were given the opportunity to experience nature first hand and to make the acquaintance of extraordinarily fascinating people.

In exchange, Fran and Hammy have amassed a tremendous knowledge of human nature, together with the ability to evaluate quickly the reliability of the reported observations and to check them themselves if necessary.

For me, work on the kestrel project began by accompanying Fran over the study-area in a VW-Bus. She tested whether I could orient myself to the compass directions and find nests with the aid of a map. We checked a few nestboxes but found no kestrels except for one dead individual at the bottom of a box. I shouted the news to Fran, standing down below, but against the fresh April wind she understood only "kestrel." She decided I needed immediate help and plunged through the ice-cold, knee-high water in a ditch, which I had already crossed, ladylike and dry, using my ladder as a bridge. Going back, we both balanced single-file over the ladder, laughing. Apart from Fran's agility at her advanced age, and her habit of letting off steam, her disregard for inclement temperature is astonishing.

When I first arrived in Plainfield in April, she trotted to the nearby pond every morning to bathe. She visited us barefoot in sandals in Germany in January, 1991, then on she went to Africa, which Hammy had always refrained from visiting because of the heat. Hammy was of more even temperament altogether, but precisely because of his unflappable personality he was no less lovable.

Perfectly composed, Hammy showed me how to band a bird—demonstrating on the dead falcon we had found! That was the extent of my introduction! Within days I was on my way alone through the marsh when I discovered a nestbox that contained my first live bird. Once again high up on the ladder, I quietly dropped the "hole-plugger"—a sponge on a long stick, used to cover the nestbox entrance—thinking I wouldn't need it. I grasped my first falcon safe in my right hand, and was all set to carry it down the ladder to the bus for banding and weighing. At that moment I spotted a second falcon in the box. Quick as thought I plugged up the nestbox hole with my right elbow. Number two was safe in there, at least. But now the first bird took firm hold of my left hand and so we stood for awhile, swaying atop the ladder—I suppose you could call it a vicious circle. With aplomb worthy of a circus actor I raised one leg and managed to whip off a shoe to plug the hole. During the next days, Fran never tired of repeating the story again and again, while Hammy merely smiled and asked me how many limbs I had.

Such unforeseen situations occurred frequently, so that improvisation was the rule rather than the exception. The frequent wracking of nerves and need to adapt were gladly suffered as a price for independent work. Fran and Hammy had realized, early on, that "spoon-feeding" and control would never have taught the gabboons to act spontaneously and independently in unusual situations—which are always cropping up when one is dealing with animals. With their antithetical methods they achieved dedication to the "own" project and keenness to work. Perhaps only those who have experienced a similar training can appreciate the procedure.

Nevertheless, it wasn't that the gabboons were left without any possibility of help, and faced with intractable problems. The Hamerstroms were always available to answer questions—except for Fran when she was busy writing one of her books—and of course they expected to be given the most detailed reports on all aspects of the project. There followed comments which ranged from severe criticism to heartfelt praise. Fran and Hammy always volunteered their frank opinion, and expected a high performance in their gabboons. This made the work in Plainfield wonderful, but also wonderfully strenuous!

That the working atmosphere was so open and personal was surely because the gabboons and the Hamerstroms lived together in this beautifully quaint house in Plainfield. It was the life of a family, and friendships developed fast

Yes, I learned a great deal in Plainfield: to wash up silver cutlery separately from the stainless-steel variety, not to put fork-handles of bone in water; to nap after lunch, to give vegetables not water to mice, to charm an owl into cheerfulness and a thousand other golden "household-rules."

Above all, however, I learned to act independently and on my own initiative, and I have the firmly rooted knowledge that people work all the more efficiently the more freedom they are given.—**Sabine Strecker, Moosbachstrasse 11, 7801 Buchenbach, Germany.**

WHY ARE YOU REALLY HERE?

There has been a recent flurry of activity in governments and universities to encourage women in science, yet some women were in science long before these special programs. It is this aspect in part we wish to discuss. Neither of us has remained in ecology but both of us are still woman scientists, perhaps in part owing to the Hamerstroms. We both had some interesting discussions, particularly with Fran, about women and their role in biology.

THE GERRARD STORY

"Why are you really here?" This is the question that Fran Hamerstrom asked me when I first met her, over twenty years ago. The question was not new to me, as many who worked in wildlife had asked me this before. The difference this time was that Fran was a woman and the others had all been men. Fran wanted to know what was going on in my life that I had showed up at her Plainfield, Wisconsin farmhouse wanting to know about her mews and about eagles. On the other hand, the men had all wanted to know what ulterior motives I had for being in the field, and they insinuated that I used my interest in wildlife biology in order to find a husband. The question, coming from Fran, was a refreshing change. The question was directed at me as a person, not as a genderized object.

That night Fran and Hammy and I talked about why I was "really there" and their enthusiasm and direction, in addition to caring and thoughtful interest in me, drew me closer to them. The next morning Fran showed me the "kestrel circuit" as we went out and banded young kestrels. That afternoon, she asked me to clean the refrigerator as the dead owl stored within had maggots. It was my first "test" and I was determined that Fran and Hammy would find no reason to judge me less highly than anyone else, male or female. Indeed, after this first test I felt totally accepted, not only as a person, but as a woman in science, one who could "hold her own."

Over time, I spent many weekends with the Hamerstroms. I never really became a typical Hamerstrom gabboon, but I often shared in the varied and fascinating life at the Hamerstroms. Sometimes I participated in observing in the field, or banding. On any visit there, I may have found another visitor, perhaps a falconer from Europe, or a raptor researcher from some other state. On one visit, I "purged" a tapeworm I had acquired from fish eaten while I was in the field banding bald eagles. I blended in and spent many hours, particularly with Fran, talking about her early years in wildlife biology, with Darlington, Leopold and others.

Fran had very strong ideas about the role of women in science and in relation to men. In the early 1970s Fran was my first role model of a woman who had entered a "man's" field and had succeeded. She awoke in me the dream that I, too, could overcome the sexism rampant in wildlife biology, and achieve what I wanted. Although I subsequently abandoned the professional career of a wildlife biologist, and went on to get a Ph.D. in Community Psychology, Fran has been my touchstone. At many times I have said to myself, as I pursued my own career interests, "What would Fran say or do?" Her work with raptors, her writing, and her ability to overcome, in her own way, the sex-role stereotypes that have oppressed women have been an inspiration for me.

I first visited Fran and Hammy because I really was interested in raptors. I really was interested in her mews. I really was interested in wildlife biology. I really was interested in meeting a human being who would accept me for all of that and nourish me as a person, as a woman in science. In recognizing all that, Fran gave new meaning to the question "Why are you really here?" and for that I will cherish her all my life.

THE SCHMUTZ STORY

I met Fran and Hammy in 1970 through Joe Schmutz, their live-in foreign summer student. Joe brought me home to meet the Hamerstroms when his VW bus broke down and needed towing. Fran and Hammy never quite believed that was why I was there. In any case, a feast was prepared—fondue on the front porch. Fran believed in welcoming people with food and Hammy enjoyed that part of all the company the most I think! Knowing Fran, pleasing Hammy may have been the primary reason she did it.

Within a short time of my arrival I was given my "test." Fran asked if I would feed the owl using part of the raccoon in the refrigerator. I know I passed the test because some twenty years later I still feel welcome when I visit the house on the marsh.

Fran and Hammy believed that couples should understand each other's work, which should also be their passion, and preferably work together. It was a great disappointment to them that I left ecology for genetics after my Master's and thereafter did not go into the field with Joe. Nevertheless I always felt encouraged by them that I too should pursue the aspect of science that was my passion. Hammy and I spent many evenings doing dishes together after one of Fran's delicious meals discussing my work and my aspirations. In his quiet way he always affirmed that he believed in me. He used to say that genetics had too many numbers for his liking but that he admired my tenacity in sticking to them. That was one of the wonderful aspects of the Hamerstroms—their nurturing of young people into science (and art) and their openmindedness even when we chose to diverge from the path they had started us along.

Fran was one of the few female role models I had in those days. All my biology professors were male then and for some years to come. I remember her advice that a woman who worked so closely with men in the field should dress as much like them as she could, with no makeup or frills. Until of course she went to a cocktail party or banquet at a conference with them where she should don her most alluring dress! She also instilled the notion that it would not be easy to be accepted as a woman and that we must try harder. Not that this was right, just that it was. Hearing this from her when I knew she supported my efforts was much easier than experiencing it with no forewarning, I believe.—**N. Gerrard and Sheila M. Schmutz, c/o Department of Animal and Poultry Science, University of Saskatchewan, Saskatoon, SK, Canada S7N 0W0.**

DEAR FRAN

I think that the circumstances of my tenure with the Hamerstroms bears repetition. While a student at the University of Wisconsin at Stevens Point, I had been "booming" twice. Then after 2 yr in graduate school in Minnesota, as I was entering an elevator in St. Paul, I heard Professor Tester say to Professor Marshall, "We need three students to go to the Hamerstroms' this weekend." I piped up, "I'll go, and I can find the other two, too." As a result of this visit, I ended up spending the summer, and 2 yr later found myself trapping Hen Harriers in Orkney with Eddie Balfour.

My reason for recounting all of that goes back to my first one-on-one contact with Hammy. After spending the dusk hours of my first field day at the Hamerstroms' on top of the Kombi alternating between spotting scope and reading in the banding book, I drove back to the house leaving the banding book topside. What a commotion that caused when it became apparent what had happened. I was delegated to tell Hammy with my head hung in shame. His words still echo, "Well you'd *better* find it!" This was not the abusive response I may have deserved, but there was no question

as to the seriousness of my transgression and the response expected from me. I still remember ironing the pages of the notebook that had gotten wet before it was found. That first evening was the beginning of the greatest learning experience of my life.

I remember so fondly the two favorite names that you called Hammy in my presence. The first was when we were looking for his approval of a manuscript or scheme, and you would refer to him as "Maestro." I feel that this was a very accurate description of his nature. He was an eminent composer, conductor and master of the art. That art was, of course, the written word, which somewhere along the line includes analytical thought as well. It is doubtful whether I or any number of gabboons would have ever written anything without Hammy's help. That help was always firm, frank, and often painful for me; but one could never say that Hammy was unkind in the process. Indeed, I can picture myself squirming in discomfort after a good "editing," and Hammy finding something so nearly absurd about my attempt at self expression that it started both of us laughing. For this, I owe Hammy much.

The other name you used for Hammy was "Gesichtelle," which literally translated means "little face." This was strictly between the two of you, but I believe it to be a term of endearment, and observed your use of it in special situations where appeasement of the "Maestro" seemed in order. Indeed, N. Tinbergen and K. Lorenz showed that this sort of behavior maintained the pair bond in many organisms. I should have learned that earlier in life.

Even as a gabboon, Hammy treated me with respect, and played the generous host beyond all expectations. We could be having a raucous writing session in the back room over a jug of MP, when Hammy could be heard, "Bill, are you in? How about you, Fran?" Usually that meant martinis for a select few before bed and the winding down of the more strenuous activities.

There are many such memories, such as the inadvertent crack left in Hammy's net door which allowed Ambrose to get into Hammy's office, the great pleasure you both took when we flew the owls indoors at night, and "mouse television." So many words added to my vocabulary: "stocking mail," "go topside," "Kombi," "George's Stomach," "do a walk-in to the nest," "Fuzz," "Cuzzin Ray" and much more.—**William C. Scharf, Biological Sciences, University of Nebraska, Lincoln, NE 68588.**

THE HAMERSTROMS, A MEMOIR

It's January and time again to throw a *bal-chatri* for wintering kestrels. The birds once more are perched on the lines in the rural areas of coastal North Carolina where I now live, but with each bird I ensnare, my mind drifts back to another day and another place—and to the always delightful company of Frances and Frederick Hamerstrom.

My recollection goes back to the Christmas season of 1973, or maybe it was 1974, when a well-used—some might say ramshackle—Volkswagen bus clattered into the parking lot at the Welder Wildlife Foundation in southern Texas. The snows and bitter cold of Wisconsin were far away once more. Fran and "Hammy" had arrived.

The Hamerstroms were a legend in their own time. I'd heard of them since my student days, of course, as had just about anyone with an interest in wildlife, but now here they were in person. Fran, hair askew, in her flannel shirt and well-worn jeans scarcely resembled the debutante and fashion model she once had been. Indeed, as I got to know her better, I suspect she gleefully "played" to the contrasts of her then-and-now image. (See page 5 of Fran's marvelous book *Strictly for the Chickens* for a photo of a *verrry* fashionable young woman poised elegantly on an impressive staircase.) Hammy, dashing in his magnificent snow-white goatee and mustache, immediately transmitted an air of quiet competence, warmth, and civility for which he was widely known (*Wildl. Soc. Bull.* 19:119–122; see also 378–379).

So, here the Hamerstroms were in person, replete with what was for me an arcane collection of wire, loops, tubes, and caged birds stored rather randomly inside and on top of their much-traveled bus. Fascinating days lay ahead.

In the winters following their so-called retirement, Fran and Hammy had begun fleeing the Pleistocene-like environment of Wisconsin, trapping and banding raptors *en route* to the more compatible climes of Texas and Mexico Harris' Hawks were their special interest while staying at Welder, before heading on to Mexico to study Ospreys, but there was always time for banding another redtail or kestrel, and certainly for discussions of Northern Harriers— Fran, I think, was one of the first to champion renaming "marsh hawks." Northern Harriers remained a special interest for Fran, although Hammy, as always, was dutifully involved with the work, whether in the field or as a reviewer of manuscripts (he was renowned for his precision with words). Fran's studies of harriers spanned some two decades and included data on more than 200 nests and almost as many color-marked breeding adults. Of the papers resulting from this volume of long-term information, one in particular stands out—for me, at least—because it clearly links the importance of prey abundance on the reproductive efforts of predators (F. Hamerstrom 1979, *Auk* 96:370–374). This work eventually led to a book-length treatment, entitled "Harrier, hawk of the marshes: the hawk that is ruled by a mouse" (1986, Smithsonian Institution Press, Washington, DC).

In Texas, the harriers and Prairie Chickens of Wisconsin were left behind in favor of Harris' Hawks. And it was

ın search of these interesting birds that I learned first hand of the paraphernalia of capturing and banding raptors. *Bal-chatris* were especially captivating for me and, more importantly, for a good number of Harris' Hawks as well. My experience with such devices was nil, and so I quickly became the newest of their many "gabboons," the Hamerstroms' quaint name for apprentices. According to Fran, "gabboon" stems from Africa, where, with a slightly different spelling, the term refers to those of a wretched tribe who are forced into servitude by a more powerful tribe. During the field season in Wisconsin, the Hamerstroms often had a houseful of such volunteer laborers at hand. Tales of the cuisine served to the gabboons, while no doubt enhanced by their repeating, nonetheless stir the workings of one's gastrointestinal system. "Roadkill stew" has since become a staple in my vocabulary, but not—I think!—as an entree on those occasions when I shared a table blessed with Fran and Hammy's cooking.

So off we went one fine day, mentors and new gabboon. Down to Kingsville, then off toward Falfurrias. Harris' Hawk country. The bus clattered, but on it went under Hammy's steady control. Fran was busy boiling water for tea on some kind of stove when Hammy spotted the first bird. Out went the *bal-chatri*; Fran lowered the trap from the moving bus with the same grace as she had descended those stairs so long ago. A quick catch. The bird was quickly ımmobilized inside a plastic tube—so that was what they were for!—again with the effortless grace that comes with long experience. Another bird along the roadside, this one with a companion nearby. With *bal-chatri* again in place, Hammy gunned down the road, turning the bus around with his own style of creative driving that comes from years of field work on narrow roads. Success again, but this time both birds wheeled to the trap and both were soon hopelessly tangled in the nooses. I'm not sure, but I'd guess that the Harris' Hawk may be the only species in which two (or more?) birds might be captured at once in a *bal-chatri*. In any case, untangling those two unhappy birds was another event etched so deeply in my memory of days long ago.

By now the water was ready, so a tea break was declared, followed by subjecting each bird to careful measurements, some of which appeared in print (F. and F. Hamerstrom 1978, *Rapt. Res.* 12:1–14). What seemed to be an unusual molting pattern, especially in the primaries, was of special interest and a good deal of time was spent examining the wings of every Harris' Hawk caught by the Hamerstroms. They had published a paper on their method of recording molting patterns (F. and F. Hamerstrom and J. Wilde, Jr. 1971, *Inland Bird Banding News* 43:107–108), and diagrams with their most current data now were stacked in the bus in a filing system whose working were known only to Fran.

Tea finished, we searched for more birds. Fran and Hammy were sharp-eyed and could spot a perched hawk of any kind with ease. My education was advancing, albeit slowly. I was to arrange the loops, opening any that had closed and setting them upright, but most of the time I just caught my fingers. The day wore on, with a tally of a few more Harris' Hawks for our effort. My work with the nooses improved, but never really to the satisfaction of Fran, who always was able to locate a misguided loop or two. Hammy just smiled—I suspect he'd witnessed a similar scene more than a few times before. And so it went.

The Hamerstroms' ventures to Texas and Mexico strained their retirement income, or at least that's what they said, so Fran used their long drives as time for writing for profit. At some point, I don't know when, she developed an interest in children's books and drew from her own experiences as a mother for material. "Walk when the moon ıs full" (1975, Crossing Press, Freedom, CA) was a result of this effort. Other experiences in their eventful lives also served as the basis for delightful stories, among them "An eagle to the sky" (1970, Iowa State University Press, Ames, IA) and "Strictly for the chickens" (1980, Iowa State University Press, Ames, IA). Scientific reports, of course, continued between these and other popular writings.

Hammy's gone now, but Fran carries on. I tried to phone her recently, just to see what she was doing, but I was unable to reach her. No doubt she still watches the prairie chickens dancing in the freshening Wisconsin spring and maybe even finds the energy to search for a few harriers' nests. I hope so. But whatever the case may be, I shall retain the rich treasure of recollections of Fran and Hammy going full force. Those, indeed, were fascinating days.—**Eric G. Bolen, The Graduate School and Department of Biological Sciences, University of North Carolina at Wilmington, Wilmington, NC 28409.**

A KESTREL TO THE SKY

An eagle's stature, of course, is much more impressive than a kestrel's. But, as Niko Tinbergen once wrote to me, kestrels are "sweet." Being highly adaptive in their behavior, these small falcons are distributed all over the World.

I have kept, bred and raised quite a lot of falcons, ıncluding European Kestrels (*Falco tinnunculus*) from in or near the town of Freiburg in southwestern Germany, American Kestrels (*F. sparverius*) caught near Plainfield, Wisconsin, and their descendants. [1,2]

When my husband, Otto Koehler, and I arrived at the Hamerstrom farmhouse in 1960, there were already five American Kestrels waiting to be taken to Europe on board the S.S. Nieuw Amsterdam—but this would be a story of

its own. There were also a Northern Harrier (*Circus cyaneus*), a Snowy Owl (*Nyctea scandiaca*) and a hand-raised Great Horned Owl (*Bubo virginianus*) that was allowed to come into the sitting room in the evening. The owl played with balls of wool like a kitten and nibbled at our ears, very gently as he probably thought.

We had some wonderful days with Frederick and Frances Hamerstrom. The first evening, Fran took me, more or less blind in the dark unknown environment, to a nearby pond and we bathed, alone under the high vault of the sky except for some turtles plunging into the water. Otto and I learned how to catch kestrels and to keep them in beer cans until they could be weighed and measured. We met Helmut Mueller and other young biologists who netted passerine birds for banding near Lake Michigan. Whatever we found dead at the roadside, squirrels and other animals, was taken home as food for the birds. When I cared for my kestrels Fred watched me silently. At last he said "She has a wonderful hand with them," which I can still hear today.

On 23 August we left for the meeting of the American Ornithologists' Union in Ann Arbor, Michigan. While on a toll highway we had a tire mishap, but Fran mastered the situation calmly smoking her cigarette. Only the kestrels were very much upset.

Next day, in Ann Arbor we met Margaret Morse Nice and her husband, whom we had visited in Chicago, Ernst Mayr, and, for the first time, Amelia Laskey. I had had some correspondence with Amelia Laskey since American ornithologists helped European ornithologists after World War II, a system organized by the Hamerstroms. We participated in the meeting for only one day. We had to go back to New York and board our ship.

In 1991, when Fran came to Freiburg again, on her way to Africa to go hunting with the pigmies, we talked about falcons and she advised me: you must write popular books, otherwise your book will never be written, with all that literature. . . . Therefore, although I still hope to publish at least some of my observations, I dare tell the story of just one of my European Kestrels in an informal paper for this Hamerstrom Issue.

The kestrel was a male named Fridolin whom I kept in an aviary for 6 yr and who afterwards lived flying free for another 7 yr using me as a food resource for himself, his mate and his young. In winter he sometimes stayed away for weeks or even months.

FRIDOLIN'S LIFE

The kestrel was brought to me as a juvenile in February 1973. I do not know his previous history. He was tolerant but not very tame. In summer he lived peacefully with an adult female in a large aviary (6 × 4 × 4 m) in Wittental, a village near Freiburg, Germany. Neither of them courted. The winter months were spent in an aviary at my house in Freiburg, and the kestrels came to Wittental again in March 1974. The male, now in adult plumage, flew

demonstratively to the potential nesting site where he called "zick-zick," but they did not get further.

After the summer of 1974, the pair stayed in Wittental all year. During winter they were allowed to use the three neighboring aviaries (all of the same size), both with and without other falcons. This gave them access to sunshine whenever possible—besides in spring, from 1973 onwards, some artificial illumination which they liked especially for warmth.

In 1975 and 1976 they had seven eggs each year. Four and three young, respectively, hatched and fledged. All eggs were fertile, but some of the chicks were too feeble to hatch. I suspect that the male brooded too long, which is a problem in raptors breeding in captivity (pers. observation). In the wild, the male has to go hunting. He relieves the female about twice every day while she feeds and preens. In the aviary he can just stay and sit until the female wants her turn. But he has no brood patches, and apparently cannot incubate adequately for long periods of time.

When the pair started to breed again in 1977, a marten (*Martes* sp.) found his way into the aviaries. On 2 May the female had disappeared.

Next spring the male courted a female Lesser Kestrel (*F. naumanni*) × European Kestrel hybrid. But when I obtained another adult female European Kestrel at the end of April 1978, he courted her and chased the hybrid. The females looked similar and behavioral differences were subtle, but the European Kestrel is the bigger species and in raptors big females seem to be attractive for males. This female, coming from a small zoo in Waldkirch where she may have been attached to another male, started laying unfertilized eggs the day after her arrival.

Neither repellents nor tasty baits in a trap box allowed me to get rid of the marten. He could no longer enter the cages, but he chased the birds from outside sometimes injuring them. Not having sufficient room for all the birds in Freiburg, I released the European Kestrels near my house at the edge of town. The birds were used to catching live prey, but, in January 1979, there was snow to worry about. None of the birds I had hacked back at the site or elsewhere, young or old, had stayed or come back and neither did the female. The male returned 3 d after release and stayed, with interruptions, for 7 yr to come.

In spring he often cached surplus mice at the wood's edge or in the garden, mostly under roots, logs and bushes, sometimes on the roof or balcony; but never more than one piece in one place. His new mate, an unidentified female to whom he had carried food for a few weeks sometimes came alone to look for his caches. How she found them is unclear. Maybe she searched the most promising structures (edges, corners, holes) which is difficult in the wood. Fran Hamerstrom suggested, he may have left some droppings. At any rate, my kestrel was breeding again, in his first year of freedom, and he did so every following year until he disappeared in February 1986.
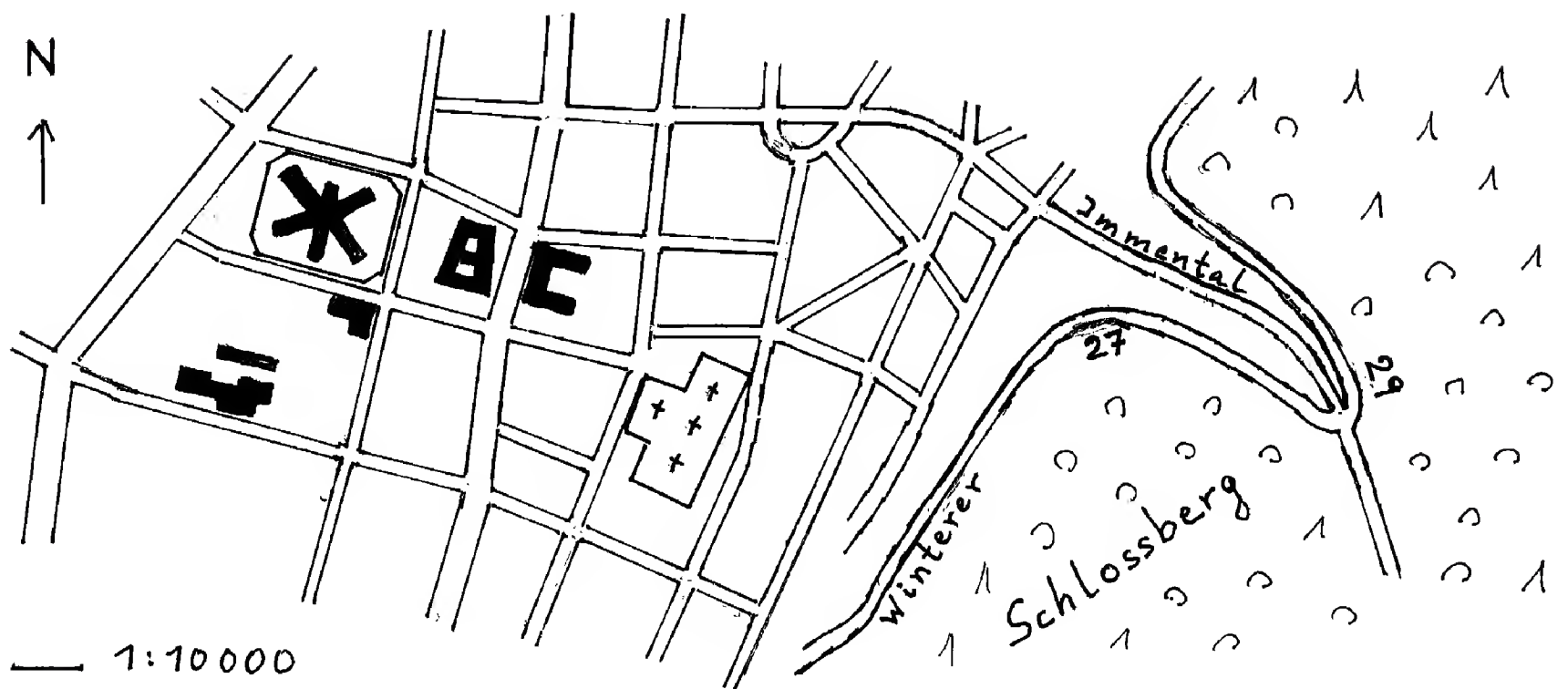
Figure 1.   Section of the map of Freiburg city. From right to left: Wintererstrasse 29 (my house), Wintererstrasse 27, old churchyard, gymnasium, Herder Publishers, the jail, north of the campus where the big Chemical—in front of small Zoological—and at the corner the Physical Institute was located.

Since Fridolin always flew in the direction of Schlossberg (Fig. 1) I suspected him to nest there in a hollow tree or on a crow's nest. I searched in vain. At last I followed him by car. He flew along Wintererstrasse up to No. 27, then headed for the city. Sometimes he landed in the trees of the old churchyard, sometimes at the gymnasium or the publisher's. I lost him from my view and though I searched these places I never found the nest. Finally, we gave him a young rat, about twice the weight of the usual mice, and then he flew straight to the jail. There were three young, about 3 wk old.

This was in June 1983. He had probably nested there since 1979 for I knew there were kestrels. At the end of July 1980, I observed a young bird twice near my house and noted: the kestrels at the jail fledged as late as this one, which probably was one of them. I now watched the male carrying white mice to his young and for proof I asked a jailer, since I was not allowed to go in, to collect some pellets: They are white, partly mixed with some gray hair of wild mice and a few chitinous remains of insects.

On 2 July 1983 after the young fledged I saw one of them tumble down and disappear from view. The female flew down toward it. This young survived the fall, but I was told that there were dogs in the yards during the night, a potential danger for fledglings.

In 1984 the kestrel had a second female and two nests on the two sides of one block with the roof between them. The secondary female was a young one.

Trios have been reported several times in European Kestrels (G. Matthäus pers. comm., W. Scherzinger pers. comm., pers. observation) and Lesser Kestrels. [3] Altenburg et al. [4] and Hamerstrom [5] have studied polygyny in harriers (*Circus* spp.) and Newton [6] lists 11 species of raptors with known cases of polygyny; these apparently depended on favorable environmental conditions, mainly food abundance.

FEEDING

Usually, I offered Fridolin live white mice on the lawn or on one of two balconies, rarely young rats or 1 d old chickens, exceptionally chicken necks or beef heart. When he felt safe, he gripped the mice at once, killed them by biting their forehead between the eyes and ears (not the nape of the neck, this by kestrels is only done with bird prey), then started for his favorite feeding place in a large beech tree. At other times he took only a few bites and carried the rest to the nest site. Sometimes he flew directly to the nest or cached his kill and came back for another mouse, on occasion repeatedly. He also caught what I threw into the air. Sometimes, when his mate or young had followed him, he presented them with food right here

By his eagerness and the number of prey items Fridolin needed, I could judge whether he had a family. During 2 yr we recorded all items (Fig. 2). The high peak in June 1984 seemed unusual. He then had two females and, unfortunately, the mice I could offer him were small, about half the weight of adults—though this is not unnatural, for in the wild young mice will be easier to catch than experienced ones. The 1985 curve seems to be more characteristic.

One day, Fridolin chased a bird, probably a Robin (*Erithacus rubecula*), nearly colliding with a car. He finally caught the bird and flew onto the roof of the house to feed

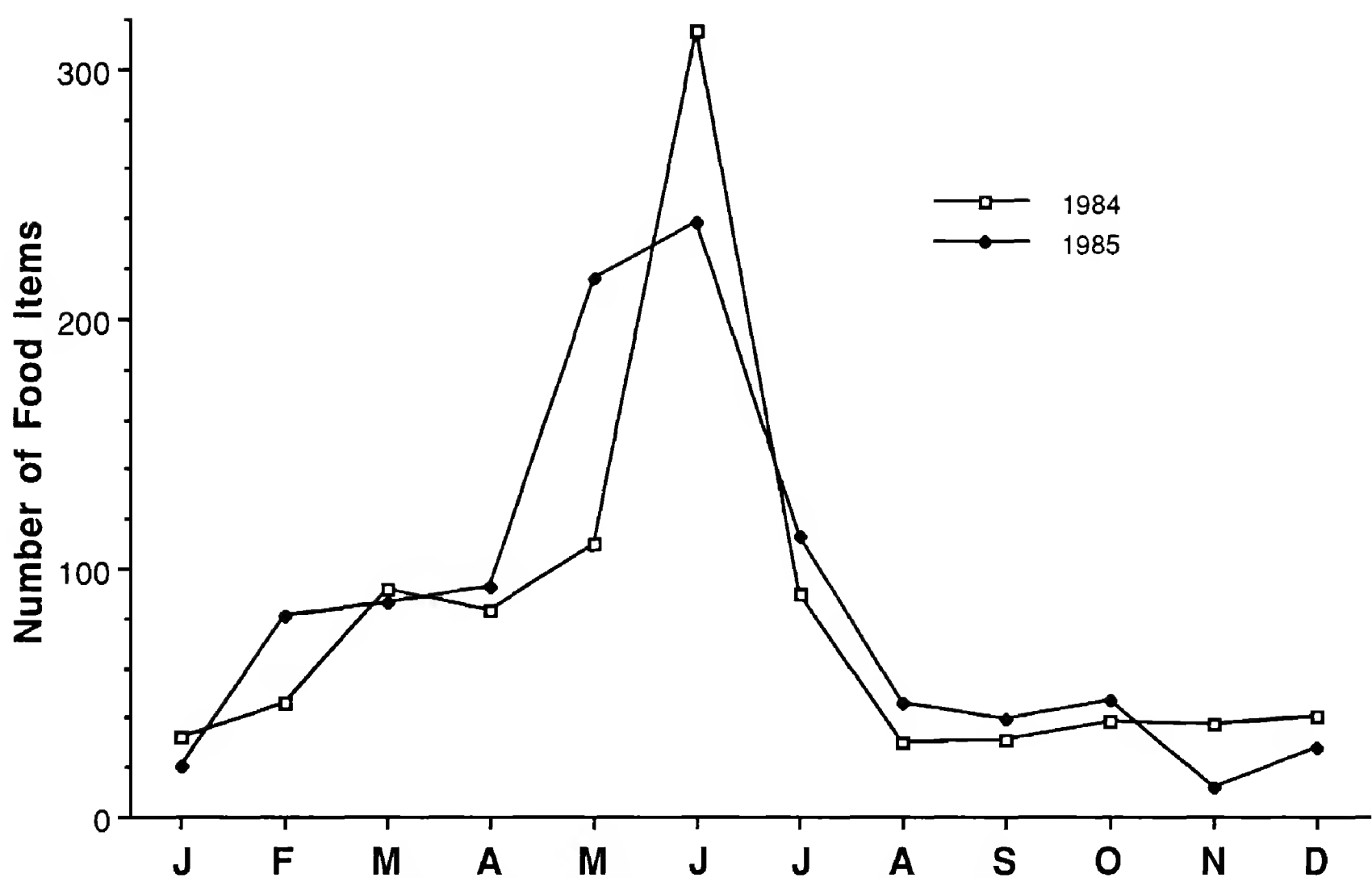He even tasted fried chicken. My dog Mira went out

Figure 2.   Number of mice and other food items taken per month in 1984 and 1985.

into the garden with part of the carcass (backbone and ribs), some meat and the lungs still adhering. She left it lying on the grass. To my surprise, the kestrel came down from his perch, settled on the chicken bones and fed, evidently enjoying his meal. Having finished, he cached the remains. This did not look similar to anything he had eaten and did not move. Mira had never served him before. How did he know it was edible?

LEARNING AND COMMUNICATION

When Fridolin had to care only for himself, he usually came once or twice in the morning and again in the afternoon, depending on daylight. While he raised young he came once more in the evening, or even throughout the day.

Until September 1984 I had a study room in the Zoological Institute. As it seems, the falcon had learned when he could expect me to be at home. He waited on his favorite perch, the tip of a very high spruce. Often he stayed there until I had come up to the house. At other times he followed me through the garden, and when he was in a great hurry he even came down to the gate, followed me into the wood where I went with the dog or even flew towards the approaching car.

The highest building on the campus is the Chemical

Institute. During courtship the pair often spent several hours a day on its flat roof and the balconies facing my window in the Zoological Institute. Thus, at times, I could keep record of what they did. But, evidently, the male observed me also. More and more frequently we arrived at home at about the same time. He could see me as I left the Institute and went to my car. No doubt he had learned that this meant I would be at home soon, and I am convinced that he sometimes followed my car.

From the roof of the Physical Institute I could watch him flying to the nesting site and back to my house. The shortest time it took him to catch two mice he brought to his mate was 5 min, with a flight distance of 1.5 km one way. He glided up the roofs and sailed to the next ones saving energy for his many flights to and from. Driving home, I sometimes saw him pausing somewhere in Immental street which, as far as I know, was formerly not his route.

Generally, he used visual signals to make me aware of his presence, when he was not able to just sit and wait Sometimes he uttered an excited "kli-kli-kli," but then, in most cases, there were dogs or crows or something else that disturbed him. It may have been also a sign of impatience, but I doubt that he intended to call me—something my Tawny Owls (*Strix aluco*), coming at night, certainly and successfully do.

COMPETITORS AND PREDATORS

Perhaps attracted by the birds in the aviary, a male kestrel used to catch mice near my house from the end of December 1969 to the beginning of April 1970. He, too, learned to wait for me at certain times and to make me aware of his presence. In later years, there were sometimes young I had raised. Other adult kestrels came only exceptionally. Thus, there was no intraspecific competition.

Red Fox (*Vulpes vulpes*), Badger (*Meles meles*), weasels (*Mustela erminea, M. nivalis*), Beech Marten (*Martes foina*) and domestic cats (*Felis catus*) visited my garden. They may have found some caches and this might have caused Fridolin to carry away his prey to some prominent buildings in his nesting area: the jail, the Chemical Institute and Herder Publishers.

Carrion crows (*Corvus corone*) sometimes waited in the trees and tried to steal what he kept in his talons. They were mobbed and chased. Once a jay (*Garrulus glandarius*) killed a mouse running in the grass while the falcon looked at it. The jay seemed to be an experienced hunter.

Blackbirds (*Turdus merula*) attacked the kestrel while they had young and for good reasons he was very cautious with them. They mobbed him furiously. Once a cock hit him so badly that he sat on the ground numb for a few seconds.

Fridolin's most dangerous interaction occurred with a buzzard (*Buteo buteo*). The buzzard had discovered that he could easily catch mice here and it was my fault not to drive him away from the beginning. Once, he stooped down onto the falcon who was attempting to catch a mouse in the grass. The kestrel was quicker and more maneuverable. The kestrel chased the buzzard extensively, but after this fearful experience he never tried to hunt as long as the buzzard was near.

AFTER THOUGHTS

There are several reports of diurnal raptors flying free [7-11] (H.-H. Beecken pers. comm.). All of these birds were kept food dependent. Otherwise, as emphasized by H. Brüll, buzzards and kestrels in their first year will go away with certainty unless they are tethered or caged before they begin to disperse in late summer or autumn.

Fridolin had been caged at that time and he had spent his second winter in an aviary near my house. He may have remembered the area when he was released at this site 5 yr later. But he was not trained and not food dependent. In winter 1980–81 he stayed away for 6 mo; he was capable of supporting himself alone.

When I last saw him on 5 February 1986 he looked healthy. Nevertheless, he may have had difficulty obtaining food. This was a hard winter. Many birds of prey starved, and the buzzard besieged us. I tried many times and trapped him at last after heavy snowfall but, probably, too late to save the kestrel.

Falconers train their birds to hunt with them. In his two-choice experiments with Red-headed Falcons (*F. chi-*

quera) W. Bednarek (pers. comm.) obtained positive results for color vision and pattern discrimination. Fridolin gave me a chance to observe how much kestrels are able to learn by themselves in their natural environment and in contact with other animals, including man. I suppose that the behavioral adaptability of kestrels partly depends on their cognitive abilities.

Similar experiences are reported by Frances Hamerstrom. [5,12] In her harrier book she writes "We are convinced that the female remembered our car, a tan Chevrolet roadster, and that she remembered it for a year. We visited her nest two or three times a day to empty the crops of her young for food-habit studies. She used to come toward the car when it was still a half mile away kekking her 'displeasure'. The next summer a female harrier came toward our car half a mile from her nest, kekking. When we borrowed Paul Errington's car, a dark Sedan, and drove along the same road, she ignored it. I am convinced this is a case of memory." And when Nancy, the eagle, was to get her freedom, Fran "left by moonlight so Nancy would not follow my car."

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HAMERSTROM SCIENCE FROM A "*Gabboon's*"[1] POINT OF VIEW

The rewards of scientific work include personal gratification gained from ingenuity, satisfied curiosity, recognition, and financial gain. Recognition by scientists of work by a peer is achieved in at least three ways: by citing a person's published paper, through awards from societies or institutions, and by attributing an idea or approach to a person.[2]

Frederick and Frances Hamerstrom have fared well in all of these recognition categories. However, because even the most valuable knowledge often is vague initially and not acquired in identifiable blocks, giving recognition can be difficult. Sometimes a "seed" for an idea is acquired but this seed can mature into a slightly different idea after nurturing. Furthermore, subtly different world views or paradigms can be acquired through someone else's influence and these can play an important role in the recipient's future. Because such subtle, conceptual acquisitions often fall through the sieve of the reward system, the purpose of this special "Hamerstrom Issue" of the *Journal of Raptor Research* is to pay tribute to recognizable and subtle contributions that Fran and Hammi[3] have made. Such contributions may have been made without the full awareness of the benefactor or Fran and Hammi.

A second purpose for this essay is to examine the Hamerstroms' approach to research from a methodological perspective. I compare what I recognize to be a Hamerstromian style in biological research to other approaches in science. My interpretation will no doubt reflect more of my own perceptions than those of Fran and Hammi, for the same reasons that science ". . . is not derived solely from what is immediately apparent to the eye and ear, but is also constructed by inference from all manner of other items of information."[4]

Having been in the forefront of a number of movements within ornithology and wildlife management according to some, the Hamerstroms have also been perceived as being on the periphery of mainstream biological science by others. Forefront contributions include, for example, the insightful study of dominance among individually marked Black-capped Chickadees (*Parus atricapillus*)[5] at a time when only loosely-conceived descriptive studies were commonplace in the ornithological literature. The Hamerstroms have championed bird and mammal trapping, marking and data recording methods; they have saved a population of an endangered subspecies, the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*), from extirpation through innovative ways; and have made several significant conceptual contributions to conservation and population biology.[6] Yet, some of their approaches have seemed unconventional, and their abstinence from certain experimental and statistical approaches puzzling. In an attempt to explain this potential paradox, I examine two features of the Hamerstroms' approach to biology: their emphasis on natural history with a reluctance to wax theoretical, and their aversion for using analytical statistics.

In Fran and Hammi's own words, "Speculation (properly labelled) has its place." While conservative with speculation, the Hamerstroms stressed the need for prediction.[7] However, the tying of observations into a theoretical knot through imaginative speculation was done sparingly by them. Hamerstrom science seems to resemble the approach of a kind of purist. Interpretation was conservatively applied and speculation disciplined. I have witnessed the Hamerstroms' insatiable interest in discussing observations of natural events and patterns in nature. It did not seem to matter whether those patterns dealt with raptor biology or with an attempt to map the location of a human gene on a chromosome, a project my wife carried out. However, I detected comparatively less interest in discussing what predictions would follow from parental investment theory or from evolutionary stable strategies. Why this reluctance to move out on a theoretical limb, when going beyond the collation of individual observations and into the formulation of general statements is an essential part of science?

Despite its considerable power, the scientific method has limitations. According to T.S. Kuhn,[8] "philosophers of science have repeatedly demonstrated that more than one theoretical construction can always be placed upon a given collection of data." Often no one single method of investigating the unknown is clearly best. Nor should any one method be easily discarded because it has limitations, as an unlucky "carpenter may reject his tools."[8] However, the most capable carpenter is the one who produces a useful product despite the limitations his or her tools might have. The carpenter who is fully aware of the limitations of the tool and able to compensate for them is likely to be the most capable in the long run. The Hamerstroms' execution of the craft has much to recommend it.

Perhaps the Hamerstroms' conservative approach to theory was because of an awareness of the limitations in the scientific way of knowing. Albert Einstein explained his view of how scientific discoveries are made.[9] His de-
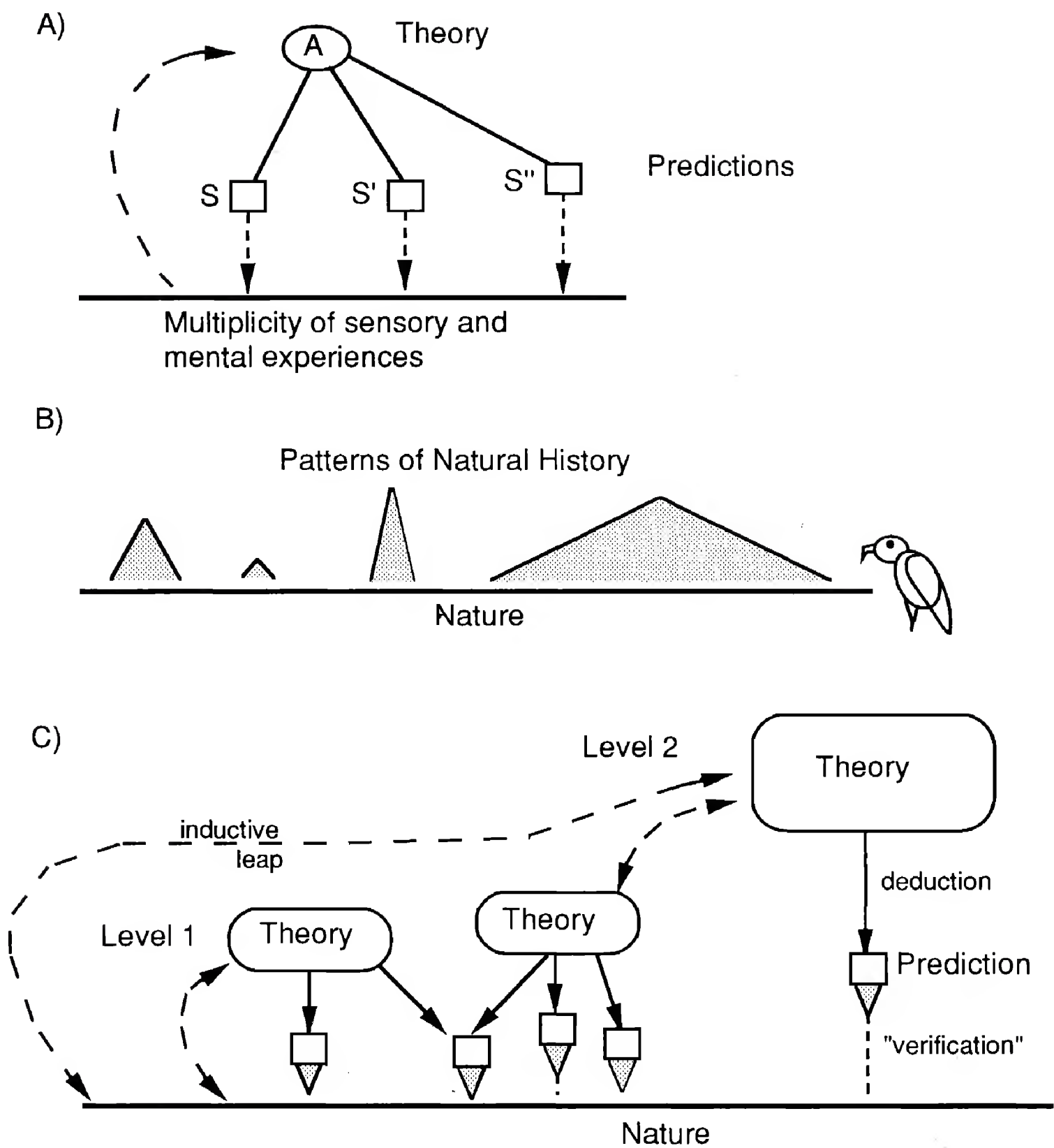
Figure 1. Three versions of how scientific discovery can be accomplished are presented. "A" is the version originally formulated by Albert Einstein, shown as adapted from G. Holton (op. cit.). Version "B" is intended to represent the Hamerstroms' style of science where data are often collected over the long term and conservatively interpreted within the context of natural history and functional ecology. Version "C" attempts to represent theoretical ecology where the source for ideas in the verification of predictions comes from theory. The connection with nature here often includes only a narrow window (e.g., short-term studies, specific data gathered; see also text).

scription went beyond the simplified textbook portrayal of the scientific method, described as hypothesis formation followed by logical deduction. Einstein recognizes four distinct components in scientific investigation which include: 1) the world around us is experienced through our senses, 2) these "sense experiences" are integrated with a person's prior conceptions and then formulated into a the-

ory using intuition (induction), 3) logical predictions are derived from these theories (deduction), and 4) these predictions are "verified" using interpretation (Fig. 1A). The deductive connection between theory and prediction may be the strongest link in the chain of scientific discovery. Verification between prediction and reality relies on a considerable amount of interpretation and thus on the

Internal Consistency within study design, methods, conclusions

External Consistency within long-term study | within species/ guild life- history | within scientific literature | within para- digm | within "personal know- ledge"
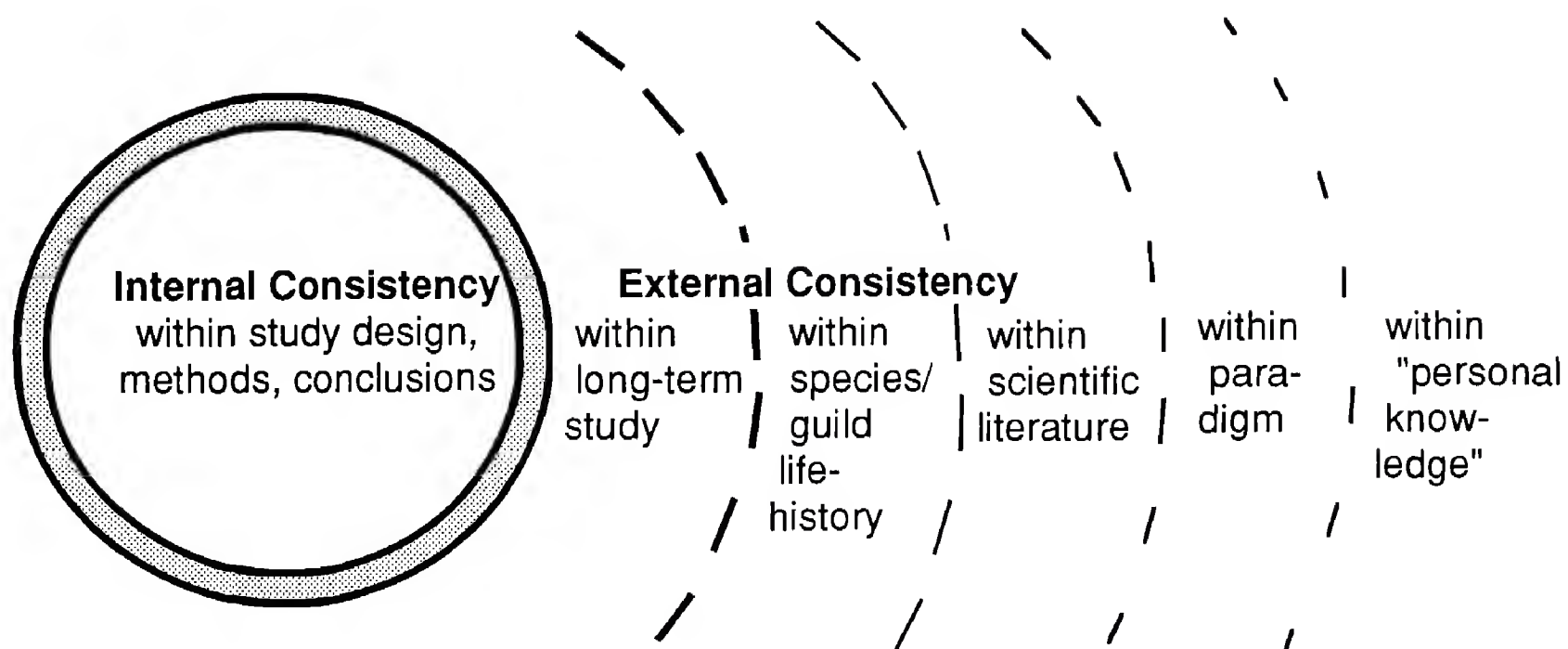
Figure 2. Different levels at which judgement of the rigor and value of an ecological investigation can be made. The levels are not mutually exclusive. See text for explanation.

accuracy of previously gained knowledge. Induction is potentially weak, because it is greatly influenced by the scientist's psychological nature. Theory is formulated through induction.

Using some or all of Einstein's components, biologists employ three identifiable approaches in research: 1) the mere description of natural events, 2) the description and explanation of repeated patterns of natural events (functional ecology) and 3) hypothesis testing. These approaches differ fundamentally. In the description of single events or patterns, the data source comes from nature. Symbolized in the form of a triangle, the triangle's base rests on the source of ideas, namely nature. The triangle's peak extends away from nature, little or far depending on the level of abstraction inherent in the interpreted explanation. The base of the triangle probably can never touch nature because the human interpreter's senses are naturally limited. These approaches (1 and 2), I believe, are compatible with the Hamerstroms' style of research (Fig. 1B). It is no coincidence that a Raptor Research Foundation award, established in the Hamerstroms' honor, recognizes individuals who have made a significant contribution to understanding the natural history of raptors.

In contrast to the description of patterns and events, in testing hypotheses the source of ideas does not come solely from nature. Ideas can be "theory-laden," derived from other theories (Fig. 1C). Testing theories that were derived from other theories and that relied on a series of *ad hoc* assumptions is not the Hamerstroms' style. When asked at the 100th annual meeting of the American Ornithologists Union in New York whether a student should concentrate on theoretical or descriptive biology, the plenary session speaker Gordon H. Orians advocated both.

In their own work, the Hamerstroms have stopped short

of formulating highly abstract interpretations. As a result, many of their data went no further than the description of patterns and basic ecological interpretations. Twenty-two years of data on the behavioral ecology and population dynamics of the Greater Prairie Chicken, perhaps one of the largest and most comprehensive data sets on a natural population, have been underused from a theoretical point of view. It would appear that the Hamerstroms have shied away from using ingenuity to formulate intellectually challenging models to account for events in nature. Not so. The Hamerstroms have not down-played the mystery in nature. Instead, they have explored mystery through visual art and poetry, and sought it in music. Fran once deplored the trend in primary and secondary schools to stress the hypothetico-deductive link in scientific investigation while down-playing the personal dimension and mystery surrounding animals. Fran and Hammi feel strongly that youths should be encouraged to experience nature first hand, both out of doors[10] and within.

Another characteristic of Hamerstrom science, in addition to a reluctance to employ abstract theory, is the reluctance to employ analytical statistics. This does not mean that the Hamerstroms are uncritical in their thinking; on the contrary, critical thinking has been a prominent feature of theirs. Although statistical analysis was not a major focus in their university education, this paucity of "training" in statistical procedure has not been the determining factor in their style. They have collaborated with first-rate statisticians including F. Hilpert, G.W. Snedecor and statisticians at the Wisconsin Department of Natural Resources. Hammi and Fran have felt that the first choice was to present data in English and with revealing, legible figures. They disapproved of "cluttering any publication with non-essential mathematics." Usually, the Hamer-

stroms have delayed publication of data until the pattern was so clear that analytical statistics seemed superfluous. As a result, their investigation has been free of the constraints that are sometimes imposed by the use of statistical tools and design.

While I personally have never fully understood the reluctance by Fran and Hammi to employ a modicum of statistical analysis, their approach is well worth consideration. The issue touches on 1) what it is that makes a scientific conclusion rigorous and 2) on the sociology of scientists.

When a reader examines a manuscript, she or he can evaluate the work at many levels. These levels can be divided into two categories: internal and external consistency. An article describing the methods, results and conclusions of some investigation might be termed internally consistent if certain widely accepted criteria are met. Such criteria can include: posing a significant biological question, choosing methods that are currently accepted by peers, using and describing the methods adequately, providing conclusions that follow logically from the methods and results, and so on. Essentially, the criteria center around possible problems with the study in an internal, narrow sense. The view is "inward" with a concentration on procedure. The Hamerstroms in my view upheld many procedural expectations which included for example an elegant simplicity in the style of writing, a clarity of presentation and the use of proper terminology.

At another level (Fig. 2), a study that satisfies all or most of the procedural queries may still not "sit well" with the reader, it may be judged somehow "externally inconsistent." I have come across no scientists that have asked whether a conclusion "feels right" as often as the Hamerstroms have. This question of feeling right has sometimes elicited glib and condescending smiles.

Many nonscientists find the observation that two scientists given the same set of data can arrive at different conclusions very disturbing. Many nonscientists and scientists alike believe that knowledge is convergent; that eventually only one and the same conclusion will survive the ultimate test. The way in which scientists gain new knowledge is complicated and more tenuous than many care to admit.

The question of whether a conclusion feels right, however, has much in common with T.S. Kuhn's[11] notion of a paradigm, a fundamental guide for scientific inquiry. According to Kuhn, paradigms bridge the understanding that has been gained in the past with questions for the future. Paradigms "are the source of the methods, problem-field, and standards of solution" (p. 103). Paradigms are larger than theories because theories "must be restricted to those phenomena and to that precision of observation with which the experimental evidence in hand already deals" (p. 100). A paradigm is far less well defined than a theory and a paradigm changes as new information is gained and old information is rejected. A paradigm

allows the independently thinking scientist to ask "What is my gut feeling about this?" By placing different levels of importance on each of a complex set of concepts contained within a "paradigmatic umbrella," scientists can legitimately arrive at different conclusions.

A paradigm, as a conceptual tool in making inferences through induction, may be situated close to the final explanation on an inspiration (least defined seed of an idea) to explanation (firmly defined concept) continuum. The remaining space along this continuum may be more aptly occupied by what M. Polanyi termed "personal knowledge."[12] The point is that knowledge does not simply flow directly from scientific "facts" and figures, but the information of knowledge involves a huge personal dimension. I believe that this personal dimension is largely ignored in most graduate student programs; it was valued and in evidence at the Hamerstrom household.

To think that only those who employ up-to-date statistical procedure carry out "good science" is flawed. The difficulties encountered in the study of complex natural events are so enormous that even approaches which are considered to be state-of-the-art by peers often are insufficient. S.H. Hurlbert[13] concluded that of 176 experimental studies published between 1960 and 1983, 27% were designed inappropriately. L.L. Eberhardt and J.M. Thomas[14] discuss the problems encountered in extrapolating from the "focal" to the larger "target" population in a reductionist approach. They pose the question "Should we, in some sense, revert to descriptive ecology?" Once more, the carpenter's tools have limitations. The chain is only as strong as the weakest link. Perhaps, the message from the Hamerstroms is not to use the term "chain" when the strength is equivalent to that provided by a "string." Much of what is considered "good science" is done not because the method warrants it or because a paradigm dictates it, but because it is considered the approach of choice by peers within one's "invisible college."[15]

The Hamerstroms have been highly independent in their thinking. They have been influenced little by the predominant "internal sociology of science"[16] or the "sociological setting"[17] which dictates scientific standards and procedures through consensus. For example, most geneticists agree that, when formulating a conclusion about heritability, gene-environment interactions need not be considered. This accepted omission is not because gene-environment interactions are not critical for the conclusion, but because the interactions are virtually impossible to measure. So, in many ways the "invisible college" has sanctioned a product even though the tools do not fully justify its production.

Hamerstrom science is reminiscent of a kind of investigation in natural history that is in danger of becoming extinct. L.L. Merrill[18] describes three views toward nature. The oldest view that prevailed for centuries is one in which things natural were romanticized; that which was natural was both beautiful and proper. Items contra-

dictory to this view were ignored. In the 19th century, naturalists began to examine carefully every possible detail in nature. Observations were no longer edited, but data were collected rigorously and descriptions made critically. Views and approaches became measured, rational and precise. While natural history and science were frequently taken to mean the same thing, the two disciplines gradually diverged. Beside the natural history investigations of animals, plants and minerals emerged distinct "pure" sciences such as geology, biology and others. While natural history examined all of nature, science studied only a part of nature. Science became preoccupied with examining theories. "But even in the very different computerized climate of the late twentieth century, natural history remains popular, as an abundance of widely read modern writers attests—Joseph Wood Krutch, Rachel Carson, Edwin Way Teale, Aldo Leopold, Henry Williamson, Gerald Durrell, Archie Carr, Annie Dillard, John McPhee, and David Attenborough, to name but a few."[17]

Whether the relations between what I viewed to be "Hamerstrom science" and the science described by theorists exist in actuality may be debated. Most importantly, however, the Hamerstroms have caused me to try and look ever deeper at nature, the process of science, and the interaction between science and the public. I thank Samuel J. Barry, Patrick Colgan, Reg Fleming, Fran Hamerstrom and Gordon H. Orians for their insightful comments on an earlier version of this manuscript.—**Josef K. Schmutz, Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada S7N 0W0.**

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[15] G. Holton, op. cit.

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Out of the Mews

I waited
until the moon slipped her silvery body
behind a cloud
Barefoot
I slid into the mews
and spoke to my eagle—softly—not loud
In the deep of the night
the jesses you made my eagle
moved onto each leg
no fright.
Oh, beautiful night.
by Fran Hamerstrom
(Reprinted from The Falconer)

THESIS ABSTRACTS

BEHAVIOR AND ECOLOGY OF POST-FLEDGING AMERICAN KESTRELS

I studied the behavior, habitat and perch use, causes of mortality, and time to dispersal of post-fledging American Kestrels (*Falco sparverius*) during spring and summer 1988–90 in central Iowa. To monitor kestrel activity, I attached radio-transmitters to 64 birds in 50 nests. All young in the study fledged from nest boxes, most of which ($N = 47$) were attached to the backs of highway signs along the Interstate-35 (I-35) right-of-way.

During the first week after fledging, kestrels spent <1% of their time foraging or flying; the remainder was spent in inactive behavior. Kestrels fledging from nests along the interstate were observed at this time primarily in cropland and along the interstate right-of-way, where they frequently perched on the ground.

Of the 16 kestrels found dead, all but 1 died during the first week after fledging, before flying skills had developed. Mammalian predation accounted for six deaths and was the main cause of mortality. Only 2 of 61 radio-marked kestrels that fledged from nest boxes along the interstate died because of a collision with a vehicle.

As kestrels grew older, perch resting decreased whereas perch hunting increased. Post-fledging kestrels fed almost exclusively on invertebrates, and mean hunting success did not exceed 55% during the 4–5 wk that birds were observed.

In 1988–89, I observed social hunting among siblings, families, and also among unrelated kestrels. Social hunting occurred during both perch hunting and ground hunting. Social foraging in these kestrels was imitative rather than cooperative.

In 1990 I observed experimentally adjusted broods of two and five post-fledging American Kestrels to test two hypotheses: 1) imitative social foraging increases the foraging efficiency of individuals in large broods, and 2) individuals in large broods will disperse sooner than individuals in small broods. No differences in foraging efficiency or in dispersal time were detected, but sample sizes were small because of high mortality or signal failure among radio-marked birds

Kestrels fledging from nest boxes along the interstate hunted extensively along secondary roads. Mean time until the initiation of dispersal of kestrels along the interstate was 22.7 d after fledging ($N = 29$, SE = 1.07, range = 9–39 d).

Band recoveries provided little evidence of natal philopatry. Only 1 of 17 birds recaptured in nest boxes as adults was banded as a nestling.—**Daniel E. Varland. 1991. Ph.D. thesis. U.S. Fish and Wildlife Service, Iowa Cooperative Fish and Wildlife Research Unit, 11 Science II, Iowa State University, Ames, IA 50011.**

RESOURCE PARTITIONING BETWEEN TWO SYMPATRIC
GOSHAWKS IN THE AUSTRALIAN WET TROPICS

Resource use by sympatric populations of the Grey Goshawk *Accipiter novaehollandiae* and the Brown Goshawk *A fasciatus* was studied in the wet tropics of northern Australia.

A morphological comparison of the two similar-sized species showed *A. novaehollandiae* is adapted for life in dense forest. The species differs from *A. fasciatus* in the shape of the wing and the size and shape of feeding structures. With a powerful bill and talons, and short but thick tarsi, it is adapted for feeding on medium-sized mammals and reptiles, and larger birds such as pigeons and megapodes.

A. fasciatus, with longer, more narrow wings, is adapted for life in more open habitats, for capturing prey in the open, and with a more delicate bill and long tarsus, possesses characters typical of bird-eating accipiters.

The diets of the two species concurred with their morphological differences. During the breeding season *A. fasciatus* took more birds than *A. novaehollandiae,* which concentrated more on medium-sized mammals and reptiles. Dietary differences during the breeding season were related to morphological differences and habitat preference of males, who were the principal food providers. During the non-breeding season there was some overlap in prey type taken by the two species and some segregation between males and females in the size of prey taken.

The hunting behaviors of the two species also differ: *A. novaehollandiae* prefers still-hunting and short-stay perch hunting, while *A. fasciatus* prefers more active foraging in addition to perch hunting.

Radio-telemetry also confirmed the implications of the morphological comparison. *A. novaehollandiae* preferred closed forests, tall open forest and tall woodland. *A. fasciatus* was most often encountered in more open habitats, but also foraged within closed forest. Both species utilized habitat edges.

The species had similar laying and fledging times; however, *A. novaehollandiae* nested in more dense habitats than *A. fasciatus*. Overlap occurred with both species nesting in tall open forest and tall woodland. *A. novaehollandiae* nested significantly closer to closed forest than *A. fasciatus*.

Nests of *A. novaehollandiae* tended to be in large spreading trees with nests placed at the end of major branches, allowing easy access. *A. fasciatus* were more catholic in their choice of nest sites and placement of nests. Differences in the overall size of nest trees were due to habitat differences: the largest trees occurred in closed forest, tall open forest and tall woodland, where *A. novaehollandiae* nested.

Ninety-four percent of *A. novaehollandiae* nests of known outcome were successful, as opposed to 62% for *A. fasciatus*. Production of young was similar between the two species, but greater nest failure for *A. fasciatus* meant that this species fledged fewer young per initial nest than *A. novaehollandiae*. Violent thunderstorms were responsible for nest failure and nestling deaths. Repetitive use of nests by both species only occurred following successful nesting.

Interspecific distances to nearest-neighbor were less than intraspecific distances. Close interspecific nesting was related to habitat heterogeneity and prey availability within the study area.

The two species clearly partitioned their resources, but the role of competition (present-day or past) in resource partitioning was unresolved. However, it was apparent that *A. novaehollandiae* (males in particular) behaviorally exclude all *A. fasciatus* from their forest patches. This active exclusion of *A. fasciatus* by *A. novaehollandiae* may be responsible for maintaining the present-day distribution of the two species where they coexist.—**Andrew M. Burton. 1991. Ph.D. thesis, Department of Zoology, James Cook University of North Queensland, Townsville, Q4811, Australia.**

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